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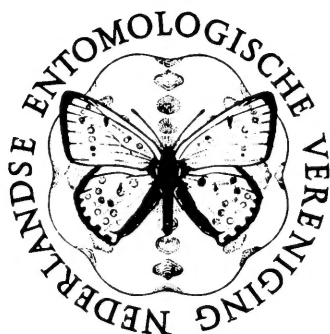




# TIJDSCHRIFT VOOR ENTOMOLOGIE

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DE NEDERLANDSE ENTOMOLOGISCHE VERENIGING



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1197  
46

# INHOUD VAN DEEL 120

Deltshev, C., zie Helsdingen, P. J. van	
Helsdingen, P. J. van, K. Thaler & C. Deltshev. — The <i>tenuis</i> group of <i>Lepthyphantes</i> Menge (Araneae, Linyphiidae) . . . . .	1
Krikken, J. — Asian bolboceratine scarabs of the genus <i>Bolbogonium</i> Boucomont (Coleoptera: Geotrupidae) . . . . .	77
Nieser, N., zie Vepsäläinen, K.	
Roskam, J. C. — Biosystematics of insects living in female birch catkins. I. Gall midges of the genus <i>Semudobia</i> Kieffer (Diptera, Cecidomyiidae) . . . . .	153
Thaler, K., zie Helsdingen, P. J. van	
Vecht, J. van der. — Studies of Oriental Stenogastrinae (Hymenoptera Vespoidea) . . . . .	55
Vepsäläinen, K., & N. Nieser. — Life cycles and alary morphs of some Dutch <i>Gerris</i> species (Heteroptera, Gerridae) . . . . .	199
Willemse, F. — A study on the genus <i>Cranaella</i> Ramme (Orthoptera, Acridoidea, Catantopinae)	109
Willemse, F. — A study on the genus <i>Cranae</i> Stål (Orthoptera, Acridoidea, Catantopinae)	121
Willemse, F. — Classification and distribution of the Sexavae of the Melanesian Subregion (Orthoptera, Tettigonioidae, Mecopodinae) . . . . .	213
Register . . . . .	279



DEEL 120

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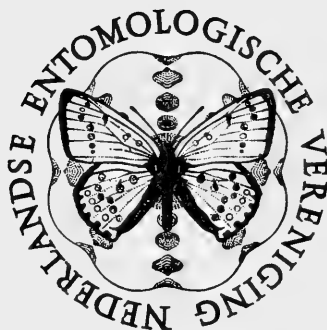
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## INHOUD

P. J. VAN HELSDINGEN, K. THALER and C. DELTSHEV. — The *tenuis* group of *Leptyphantes* Menge (Araneae, Linyphiidae), p. 1—54, fig. 1—69.





# THE *TENUIS* GROUP OF *LEPTHYPHANTES* MENGE (ARANEAE, LINYPHIIDAE)

by

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With 69 text-figures

## INTRODUCTION

Within the Linyphiidae, the genus *Leptyphantes* is one of the largest. It is rich in species, which are found in a wide range of habitats, from the Arctic in the north to the Mediterranean in the south, at high altitudes in the Alps as well as in the lower parts of Europe. In Asia, North America, and Africa they occur in comparable situations. A number of species have also been described from other parts of the world, but at least some of these we may regard sceptically. Even with this restriction there is an overwhelming amount of species and the genus is notorious for that very reason. The inaccessibility of the genus is aggravated by the many poor descriptions without, or with inadequate, illustrations.

Several authors have tried to arrange the species into natural, monophyletic groups. One of these groups, the *tenuis* group, will be discussed in this paper. As already pointed out by Wanless (1973: 139), this group is not sharply limited. Notably species as *L. alacris* (Blackwall) and its near relatives are, at least morphologically, close to the *tenuis* group, but for practical reasons we have restricted ourselves to the species-group as delimited by Simon (1929, "4e Groupe", p. 589), Locket & Millidge (1953, "Group III", p. 384), and Wiehle (1956, "IV. *Tenuis*-Gruppe", p. 191). We have included as many species as possible which from their descriptions, and above all from the illustrations, could be referred to this species-group. Inevitably some may have escaped attention, because the available descriptions lacked any indication of their belonging to the group dealt with here.

Many species of the *tenuis* group are very common and widely distributed, and every ecologist will collect large series of certain species in his pitfalls or through hand-collecting. Still the identification even of the common species is far from easy, because the palps and epigynes are very small, while the characters

commonly used for recognition of the species are found in the shapes of the different elements of these organs. The shapes vary with the angle of vision and even a slight expansion of the haematodocha, as it is sometimes found in preserved specimens, may present a very different picture. As a rule, the major collections examined in recent years contained many a misidentification, a clear demonstration of the difficulties presented by this group. It also compels us to make a very critical use of literature records.

It was thought to be helpful to give a summary of all known species of this group, presenting also their diagnostic characters, their geographical variations, their distributions and ecological requirements (where possible). Wanless (1971) already published a series of excellent illustrations, photographic pictures and line-drawings, of the epigynes of the West-European species. They are of great help and one realizes how badly similar figures of the male palps are needed. If all former descriptions had been furnished with such illustrations, a revision of *Lepthyphantes* would have been a less time-consuming task.

The main object being to expound our modern views concerning this group, we nevertheless have also tried to bring the nomenclature up to date. The present situation is far from satisfactory in view of the fact that many of the older names were listed as synonyms by authors such as Blackwall, Thorell and Pickard-Cambridge. Apparently they were in contact with each other from time to time, as Thorell, for instance, actually was able to compare many examples of Blackwall's species with his own specimens. This often resulted in the recognition of synonymies, and from then onward a name could be unanimously treated as such. The difficulty lies in the supposition, or near certainty, that recognition of species was a matter of general appearance rather than of a study of the genitalia, stridulating files and other structural characters we now consider of paramount importance. This latter method started with Blackwall, Kulczyński, and Simon, but we still have to deal with an inheritance of species described with the use of coloration and abdominal patterns only and listed as junior synonyms of currently used names. It is beyond our possibilities to evaluate the earlier decisions, given mainly by Kulczyński and Chyzer & Kulczyński. However, a re-examination of some of the old collections gives one the strong impression that the recognition of many of the *Lepthyphantes* species proved to be difficult even to the more advanced arachnologists. Too many series were found to consist of more than one species. It makes it the more important to stabilize the present situation by procuring useful means for the identification of the species.

### THE *TENUIS* GROUP

- Leptyphantes*, 4e Groupe, Simon, 1929: 589.  
*Lepthyphantes*, Group III, Locket & Millidge, 1953: 384.  
*Lepthyphantes*, IV. *Tenuis*-Gruppe, Wiehle, 1956: 191.  
*Lepthyphantes*, Group 1(a), Wanless, 1973: 139.

Within the large and rather heterogeneous genus *Lepthyphantes* the *tenuis* group has been recognized by most authors as a distinct group. It can be easily distinguished from most of the other currently recognized species-groups, though

Wanless (1973: 139) indicated the weak points in the system of grouping. He suggested a much finer subdivision of the genus into species-groups and subgroups, at the same time pointing out the transitions from one group to the other. In his grouping of the species — working with the British species and basing his conclusions on a study of the female genitalia only — all species usually referred to the *tenuis* group are kept together in his group 1(a), while *L. alacris* (Blackwall) (group 1 (b)), and *L. leprosus* (Ohlert) and *L. minutus* (Blackwall) (group 1 (c)), are thought to be very closely related to the *tenuis* group proper. These three species have an epigyne comparable in structure to that of *tenuis*, but it is larger and more complicated. It is our present opinion that *cristatus* takes a rather isolated position within the *tenuis* group and shows an affiliation with the three species placed near the *tenuis* group by Wanless.

Though recognized by most authors as a homogeneous species-group, it is not easy to delimit the group clearly. Our diagnosis is given below. Without a detailed study of the other species-groups it cannot but have its imperfections.

Diagnosis of the *tenuis* group. Comparisons with other species-groups are given in square brackets.

Medium-sized animals (1.7—4.1 mm) in comparison with the other species-groups of the genus. Abdomen of female with a dorsal pattern of transverse blackish bars and white blotches on the intervening areas, and with light or white longitudinal lateral band [cf. *pallidus* group, where faint bars may be present]; pattern obscure in the male. Chelicerae with three dorsal and three ventral teeth, slightly modified in the male; stridulating files always present. Femora spineless with the exception of a prolateral spine on femur I. Tibia I with one pro- and one retrolateral spine, tibia II with one retrolateral spine, in addition to the two dorsal spines; tibiae III and IV without lateral spines (but with one retrolateral spine in *cristatus*); no ventral spines present [cf. *L. expunctus*, *mughi*, etc.]. Metatarsi with a single dorsal spine (but with several spines in *spiniger*) [cf. *nebulosus* group, where several spines are present]. Tm I (0.15—) 0.20—0.25 (—0.30) [cf. *obscurus* group]. Male palpal tibia with one spine (or more: *cristatus*), which is at least as strong and long as the patellar spine [cf. *obscurus*, *pallidus*, *expunctus*, *mughi*, and related species]. Cymbium rather simple, without tubercles or horns (but with small tubercle in *cristatus*) [cf. *obscurus* group, *nebulosus* group]. Epigyne moderately large, not much protruding from the ventral surface of the abdomen [cf. *nebulosus* group]. Scape simple-folded [cf. *alacris*, where it is invaginated, see Wanless, 1973: 141, figs. 24D—E].

General structure of the secondary genitalia.

Male palp (Fig. 3, 5). — Cymbium (*c*) not modified, except in *cristatus*, where a basal latero-dorsal projection is present. Paracymbium (*pc*) relatively simple in comparison with other species-groups within the genus; distal branch of the roughly U-shaped element ending in a flat, blade-like tip; in most species one or more teeth present on basal branch or middle section. Haematodocha and tegular section without diagnostic features on species level; median apophysis (*ma*) always with acute tip, which points outward just below tip of cymbium (generic

character). All other elements attached to each other and to radix by membranes, forming together the radical complex, which looks rather rigid in its mutual cohesion. Radix (*r*) always distinctly curved, other elements implanted on basal and concave middle part (as oriented in the unexpanded palp). Lamella (*l*) in most species S-shaped, membranous or lightly sclerotized, free tip usually incised, forked, or composed of several branches; element conspicuous in lateral aspect. Embolus (*e*) a sinuous element which broadens out halfway into an often dentigerous protrusion, then, after a narrow middle section, widens into a more voluminous apical section, which is bifid, one of the tips being the spermduct-tooth. Terminal apophysis (*ta*) consisting of membranous sclerites and chitinous tooth or teeth, situated between embolus and lamella. Embolic membrane (*em*) small, covering tip of embolus in the unexpanded palp.

Main diagnostically important characters are: positions and size of tooth or teeth on paracymbium; shape of lamella; absence, presence, number, and size of teeth on basic section of embolus.

Epigyne (Fig. 1, 2). — Essentially not differing from general structure of this organ in other species-groups of the genus (see Wanless, 1973, for a schematic representation of different degrees of complexity). Atrium surrounded by more or less unmodified, sclerotized anterior and lateral walls; atrium bordered posteriorly by the posterior median plate (*mp*) (subgenital sclerite of Wanless), which in all species of the *tenuis* group is deeply incised medially; lateral margins of posterior median plate in posterior view of the uncleared epigyne indicated by the two darker (more sclerotized) fertilization-ducts. Atrium for the major part covered by the scape, which runs from its base on the anterior wall of the atrium in posterior direction; scape in all species of the *tenuis* group composed of a more or less straight basal part, reaching as far as the posterior median plate, then rather abruptly curving to the dorsal side and forward again (inside, and out of view) and continuing as a second, arched, inner section, the stretcher (*st*) on the extreme tip reaching the posterior side of the epigyne just between transition of basal into arched section and posterior median plate; stretcher always visible in the ventral aspect at the posterior tip of the visible scape as a round, protruding knob and furnished with a pit or socket; ventral aspect of epigyne allowing of a view of the exposed basal part of the scape, bordered at either side by the lateral wing-like extensions of the first part of the arched, second section of the scape, which in most species is distinctly wider than the anterior half of the basal part of the scape, and often of characteristic shape. In the unexpanded or uncleared epigyne, the tip of the arched part of the scape remains invisible, with the exception of the stretcher; on this tip are to be found two lateral sockets (see below) and, slightly more medially, the entrances of the two spermducts, which run from these pores symmetrically and often parallel through the whole length of the scape and the anterior and lateral walls of the atrium, each curving to its own side, to the receptacula seminis.

Functional aspects. — A general understanding of the functioning of the type of secondary genitalia found in this species-group may be obtained by comparison

of the structures found here and in *Lepthyphantes leprosus* (Ohlert), a representative of another species-group. The functioning of the genital organs in the latter species have been studied by one of us (Van Helsdingen, 1965), and though we should be aware of the dangers that attach to a too hasty generalization, we may safely assume at least some of the elements to function in a similar way.

The presence in the epigyne of a long, curved scape and a characteristically built male embolus (with its typical, voluminous, double-tipped and at one side grooved apical section), most probably correlate with each other: in functional contact the curved part of the scape is pulled around the apical section of the embolus in such a way, that one tip of the embolus fits into one of the lateral sockets at the tip of the scape (when the left palp is used it is pushed into the left socket, and vice versa), while the other tips, the spermduct-tooth, disappears into the entrance of the female spermduct at the same side of the scape. The scape is pulled out and kept in place by means of the median apophysis, the tip of which element grips the stretcher at the tip of the scape, using the socket at the stretcher's knob-shaped tip as a foothold, during the very first moments of contact between palp and epigyne. Leaving the movements of the different elements out of consideration, we may assume to find, in the final situation, the male palp firmly anchored on the epigyne through the combined forces of the paracymbium (anchored on the scape), the radix (on the scape), the terminal apophysis (within the atrium and on the posterior median plate), and the lamella (on the posterior median plate, in co-operation with the terminal apophysis). Whether the scape is lifted out of its resting position and twisted sideways, as was observed in *L. leprosus*, is questionable, but, though likely, not necessarily the case. It would be very interesting to learn what variations are possible on the theme found in *leprosus*, not only in order to understand the intricate movements of the scape, but also to find out the possible function of the tooth, or teeth in some species, on the paracymbium.

#### KEY TO THE RECOGNIZED PALAEARCTIC SPECIES

##### Males

1. Palpal tibia with four spines, cymbium with a dorso-lateral tubercle near its base (Fig. 52) . . . . . *cristatus* (p. 40)
- Palpal tibia with a single spine, cymbium without a dorso-lateral tubercle near its base . . . . . 2
2. Posterior margin of paracymbium with tooth or teeth . . . . . 3
- Posterior margin of paracymbium without tooth, or, at the most, with a ridge . . . . . 12
3. Paracymbium with small tooth at posterior margin only (Fig. 9) . . . . . 4
- Posterior margin of paracymbium with a large tooth (Fig. 47); or posterior margin with two teeth (Fig. 33); or a second tooth present at anterior margin of basal branch (Fig. 18) or at base of distal branch (Fig. 36) . . . . . 9
4. Length of cephalothorax 0.95 mm or less . . . . . 5
- Length of cephalothorax 0.95 mm or more . . . . . 7
5. Embolus without denticles . . . . . 6
- Embolus with denticles along ventral margin of basal section . . . *perseus* (p. 11)

6. Stridulating files fine (Fig. 55); chelicerae without latero-basal boss; lamella sickle-shaped (Fig. 5) ..... *mengei* (p. 8)
- Stridulating files coarse and often obscure (Fig. 56, ♀!); chelicerae with latero-basal boss (Fig. 12); terminal and subterminal parts of lamella more straight, not sickle-shaped (Fig. 9) ..... *flavipes* (p. 12)
7. Metatarsi with one dorsal spine only; basal section of embolus with 7 denticles or less ..... 8
- Metatarsi with several spines; basal section of embolus with about 11 denticles (Fig. 29); lamella (Fig. 28) with longest branch forked at tip; stridulating files very fine (Fig. 62) ..... *spiniger* (p. 27)
8. Stridulating files very coarse (Fig. 60); basal section of embolus with 4 denticles (Fig. 23); dorsal branch of distal part of lamella bluntly truncated (Fig. 22) ..... *drenskyi* (p. 22)
- Stridulating files less coarse (Fig. 61); basal section of embolus with 7 denticles (Fig. 26); small tooth at posterior margin of paracymbium pointing backwards (Fig. 27) ..... *zimmermanni* (p. 23)
9. Larger specimens (length cephalothorax 1.2 mm or more); tooth at posterior margin of paracymbium large (Fig. 47); distal branches of lamella diverging (Fig. 47); stridulating files fine (Fig. 67) ..... *nigriventris* (p. 36)
- Smaller specimens (length cephalothorax 1.1 mm or less) ..... 10
10. Only one tooth present at posterior margin of paracymbium ..... 11
- Two teeth at posterior margin of paracymbium (Fig. 33) . . . *floriana* (p. 28)
11. Large second tooth present on paracymbium just inside distal branch (Fig. 36); lamella large but simply curved (Fig. 36) ..... *tenebricola* (p. 30)
- Small second tooth on paracymbium situated at anterior margin of proximal branch (Fig. 18); lamella smaller, with bluntly tipped dorsal branch (Fig. 18) ..... *tenuis* (p. 17)
12. No tooth present on paracymbium (Fig. 20); cephalothorax with a dark median vitta ..... *tenebricoloides* (p. 21)
- Paracymbium with distinct tooth, large or small ..... 13
13. Paracymbium with a denticle near anterior margin of proximal branch (Fig. 13); specimens small (length cephalothorax 0.9 mm or less); lamella (Fig. 13) hardly curved ..... *herbicola* (p. 16)
- Paracymbium with a large tooth near base of distal branch; specimens larger ..... 14
14. Distal branches of lamella parallel (Fig. 45); stridulating files fine (Fig. 66) ..... *jacksonoides* (p. 34)
- Distal branches of lamella distinctly diverging (Fig. 39); stridulating files rather coarse (Fig. 65) ..... *jacksoni* (p. 32)

#### Females

1. Tibiae III and IV with an I-spine in addition to the two d-spines; epigyne, Fig. 54 ..... *cristatus* (p. 40)
- Tibiae III and IV with the usual pair of d-spines only ..... 2
2. Visible basal section of scape with a medial pit (Fig. 49, 51), or with a

- depression near the broadened tip (Fig. 42, 46) . . . . . 3
- Visible part of scape without a medial pit, nor with a depressed area near its tip . . . . . 6
3. Basal part of scape with a medial pit (Fig. 49) . . . . . 4
- Basal part of scape with a depressed area near tip (Fig. 42) . . . . . 5
4. Larger specimens, with length of cephalothorax more than 1.20 mm, femur I 1.5 mm or longer: two (sub)species which differ only slightly in the shape of their scapes (Fig. 49 and 51) and in their provenance . . . . .
- . . . . . *nigriventris* (p. 36) and *camtschaticus* (p. 38)
- Smaller specimens: length cephalothorax less than 1.20 mm, femur I not longer than 1.30 mm; scape of epigyne with a transverse, pigmented (sclerotized) ridge at transition of exposed basal part and curved inner part (Fig. 38); medial pit not always present (see also couplet 8) *tenebricola* (p. 30)
5. Stridulating files rather coarse (Fig. 65) . . . . . *jacksoni* (p. 32)
- Stridulating files finer (Fig. 66) . . . . . *jacksonoides* (p. 34)
6. Visible part of scape gradually widening with concave margins from base to posterior end, without parallel-sided anterior section, the margins reaching broadest point of scape without any interruption . . . . . 7
- Visible part of scape roundish or with lateral lobes, not gradually widening with concave margins, but often with a distinctly parallel-sided anterior section; or, if gradually widening, then lateral margins not reaching broadest point of scape without any interruption . . . . . 9
7. Larger specimens: length cephalothorax 1.25—1.55, length femur I 1.50—1.80 mm; cephalothorax with a dark grey median streak, abdomen with paired black spots, otherwise light; stridulating files rather fine (Fig. 59) . . . . .
- . . . . . *tenebricoloides* (p. 21)
- Smaller specimens . . . . . 8
8. Scape with distinct, more sclerotized, transverse ridge at posterior margin of exposed part; most specimens with a trace of a medial depression or pit at half length of scape, in some specimens this pit distinctly developed (Fig. 37 and 38) (see also couplet 4); posterior median plate not much broader than scape; lateral lobes of inner part of scape with convex margins; width of scape 0.17—0.22 mm . . . . . *tenebricola* (p. 30)
- Scape without distinct transverse ridge; posterior median plate distinctly wider than scape; lateral lobes with concave margins (Fig. 15); width of scape 0.12—0.15 mm . . . . . *herbicola* (p. 16)
9. Scape with parallel-sided basal "stem" or gradually widening in posterior direction . . . . . 10
- Exposed part of scape with lateral lobes near base, or broadly rounded . . . . . 13
10. Scape distinctly anchor-shaped, with narrow, parallel-sided "stem" gradually widening into transverse posterior part; inner, curved part of scape visible as strongly rounded lobes; posterior median plate not much wider than scape (Fig. 16); width of scape 0.13—0.15 mm; stridulating files rather coarse (Fig. 58) . . . . . *tenuis* (p. 17)
- Lateral lobes not rounded . . . . . 11

11. Metatarsi with more than one spine; stridulating files very fine (Fig. 62) ..... *spiniger* (p. 27)
- Metatarsi with a single d-spine; stridulating files not very fine ..... 12
12. Lateral lobes of inner part of scape with rather even concave margin towards broadest point, from there curved inward (Fig. 24); scape slightly narrower than in next species (width of outer scape 0.150—0.175, of inner scape 0.150—0.175 mm) ..... *zimmermanni* (p. 23)
- Lateral lobes with a small but distinct projection just in front of broadest point, hence margin in front of broadest point not evenly concave (Fig. 34); scape slightly wider than in former species (width of outer scape 0.175—0.190, of inner scape 0.185—0.200 mm) ..... *floriana* (p. 28)
13. Exposed part of scape with lateral, wing-like extensions on anterior half (Fig. 4); stridulating files fine (Fig. 55) ..... *mengei* (p. 8)
- Exposed part of scape more or less evenly rounded, i.e. without incisions and without distinct, more or less parallel-sided basal "stem" (Fig. 11); stridulating files very coarse, hardly visible (Fig. 56) ..... *flavipes* (p. 12)

### ***Lepthyphantes mengei* Kulczyński**

(Fig. 3—5, 55)

*Lepthyphantes mengei* Kulczyński, 1887: 267, 320, Pl. 7 Fig. 37—39 (descr. ♀ ♂; Poland). Miller, 1947: 26, 29, 40, 79, Pl. 12 Fig. 8—11, 14, Pl. 13 Fig. 1 (♀ ♂). Locket & Millidge, 1953: 388, Fig. 231 A, C, E, 232 C, D (♀ ♂). Wiehle, 1956: 202, Fig. 340—344 (♀ ♂). Wanless, 1971: 22, 26, Pl. 2, Pl. 6 Fig. F (♀); 1973: 129, 134, Pl. 1 Fig. 6, Pl. 6 Fig. 6 (♀).

*Lepthyphantes gallicus* Simon, 1929: 591, 594, 734, Fig. 906—907 (descr. ♀ ♂; France). Jackson, 1930: 653 (= *mengei*).

*Linyphia concinna* L. Koch, 1879: 37, Pl. 1 Fig. 26 (descr. ♀; Siberia). Preoccupied by *Linyphia concinna* Thorell, 1875 [= *Centromerita concinna* (Thorell)].

*Linyphia tomskica* Strand; Ermolajev, 1934: 130 (nom. nov. pro *Linyphia concinna* L. Koch, 1879).

*Linyphia concinnella* Roewer, 1942: 578 (nom. nov. pro *Linyphia concinna* L. Koch, 1879).

*Lepthyphantes concinnus*; Holm, 1945: 8, 56 (as senior synonym of *Lepthyphantes mengei* Kulczyński).

**Remarks.** — Despite the recent discovery (see Locket, Millidge & Van Helsdingen, 1970: 90) that the type-series of *Linyphia tenebricola* Wider, 1834, belongs to the species currently known as *Lepthyphantes mengei* Kulczyński, 1887, we maintain the name commonly used before that discovery. A proposal to stabilize this situation has been presented to the International Commission on Zoological Nomenclature. See also under remarks on *Lepthyphantes tenebricola* (Wider).

Both Strand and Roewer published replacement names for *Linyphia concinna* L. Koch, 1879, because it was preoccupied by *Linyphia concinna* Thorell, 1875. Holm (1945) re-examined Koch's material and found it to be synonymous with *Lepthyphantes mengei*. However, by placing *L. mengei* as a junior synonym of *Lepthyphantes concinnus* he forgot to deal with the problem of the preoccupation. Subsequently he corrected this error by placing *L. concinna* as synonym of *mengei*, the only valid solution.

The original material of *Linyphia concinna* L. Koch (1♂ 2♀) is preserved in Stockholm (NRS). Original material of *Lepthyphantes gallicus* Simon could not be





Fig. 1—2. Schematic representation of epigyne in *Lepthyphantes*. 1, ventral aspect; 2, lateral aspect (*mp*, posterior median plate; *st*, stretcher).

Fig. 3—5. *Lepthyphantes mendei* Kulczyński. 3, radical section of male palp, ventral aspect; 4, epigyne; 5, male palp, lateral aspect (*c*, cymbium; *e*, embolus; *em*, embolic membrane; *l*, lamella; *ma*, median apophysis; *pc*, paracymbium; *r*, radix; *ta*, terminal apophysis). 3, X 440; 4, X 225; 5, X 180

traced with any certainty, but all material in the Simon collection under that name has been examined (MP). Neglecting the presence of a few specimens of other species — a not unusual sample pollution of *Lepthyphantes* in old collections — all *gallicus* material belongs to *mengei*, and Jackson's (1930) statement can only be confirmed.

Diagnosis. — *L. mengei* belongs to the smaller species of the group. The fine stridulating files distinguish it at once from *L. flavipes* (Blackwall), the shapes of the lamella and epigyne are quite characteristic.

Measurements (in mm). Total length, ♀ 1.9—2.5, ♂ 1.8—2.2; length cephalothorax, ♀ 0.80—0.92, ♂ 0.80—0.95. Legs: Fe I 1.15—1.30 times length cephalothorax in ♀, 1.20—1.35 in ♂.

Stridulating files fine (Fig. 55).

Male palp (Fig. 3,5) characterized by the comparatively obtuse (if compared with *flavipes*) tooth on the posterior margin of the paracymbium, the sickle-shaped lamella which is provided with a dorsal lobe, the tongue-shaped structure of the terminal apophysis as seen in the lateral aspect, and the absence of denticles on the basal part of the embolus. The tooth on the paracymbium lies rather far to the ventral side. Length of cymbium 0.28—0.37 mm.

Epigyne (Fig. 4). Basal part of scape roughly anchor-shaped but anterior portion furnished with lateral wings, which slightly protrude in ventral direction; inner part of scape visible as a slightly projecting lobe at either side of the scape in the incisions between tips of anchor and lateral wings; stretcher as usual. Posterior median plate hardly wider than scape. Width of basal part of scape 0.12—0.15, of posterior median plate 0.13—1.17 mm.

Distribution. — Bonnet could list the species from most European countries within the following boundaries: the British Isles, Iceland, Scandinavia, the European U.S.S.R. and West Siberia, the Balkans, Austria, Switzerland, and France. It has also been recorded from Greenland (Bonnet, 1957: 2432), but this was proven to be incorrect (Braendegård, 1958: 87). Recent records, later than 1940, include again Siberia (Holm, 1970), Finland (Lehtinen & Kleemola, 1962; Huhta, 1965, 1971; Palmgren, 1972), Estland (Vilbaste, 1973), Lapland (Holm, 1945, 1952, 1959), Iceland (Cloudsley-Thompson, 1948; Braendegård, 1958), and most other countries within the boundaries mentioned.

A cave record from Rumania (Denis, 1952: 12) was based on four specimens (MP, re-examined) which appeared to belong to *L. flavipes* (Blackwall).

We have studied material from Austria (Tirol, Osttirol, common), Czechoslovakia (Böhmen, common), Switzerland (Schwyz, Glarus, Engadin), northern Italy (Bergamo, Lago di Garda, up to 1800 m), Holland (common), Norway (specimens in coll. Strand, MP), and Iceland (MP). We could also re-examine the numerous specimens from the Paris collection (many with labels bearing the name *L. gallicus* Simon!). Figures based on specimens from Holland.

*L. mengei* thus seems to be absent from mediterranean Italy and from Spain, Portugal and Greece. In the north it far exceeds the distribution of *L. flavipes* (Blackwall), and the occurrence in Iceland, Lapland and Siberia shows an ability

to survive in subarctic regions. In the Alps (and Pyrenees?) it has been found at higher elevations (up to 1800 m) than *flavipes* (up to 1200 m), demonstrating the same climatic tolerance.

In Central Europe it is one of the commonest species of the *tenuis* group. It occurs in leaf-litter, moss, sphagnum, and under stones. Adult specimens are found at all seasons (Braun & Rabeler, 1969: 43; Palmgren, 1975: 60).

***Lepthyphantes perseus* Van Helsdingen, spec. nov.**

(Fig. 6—8, 69)

Holotype: ♂, from Iran, Assalem, 2300 m, beech forest, v.1975, Ressler leg.; 2♂ paratypes from same locality (holotype in SMF, paratypes in personal collection of J. Wunderlich and ML).

The three above specimens were entrusted to us for inclusion in our present paper by Mr. J. Wunderlich of Neuenburg, Germany. Originating from a hardly investigated region as Iran they are of great interest. The specimens much resemble *mengei*, but differ in the shape of the lamella, terminal apophysis, and in the dentition of the embolus. In size, coloration, cheliceral dentition, and stridulating files there are hardly any differences between these species. On the basis of the observed differences we treat this taxon as a separate species.

Measurements (in mm). Male. Total length 1.8—2.05, length cephalothorax 0.82—0.87. Legs: Fe I 1.20—1.35 times length cephalothorax.

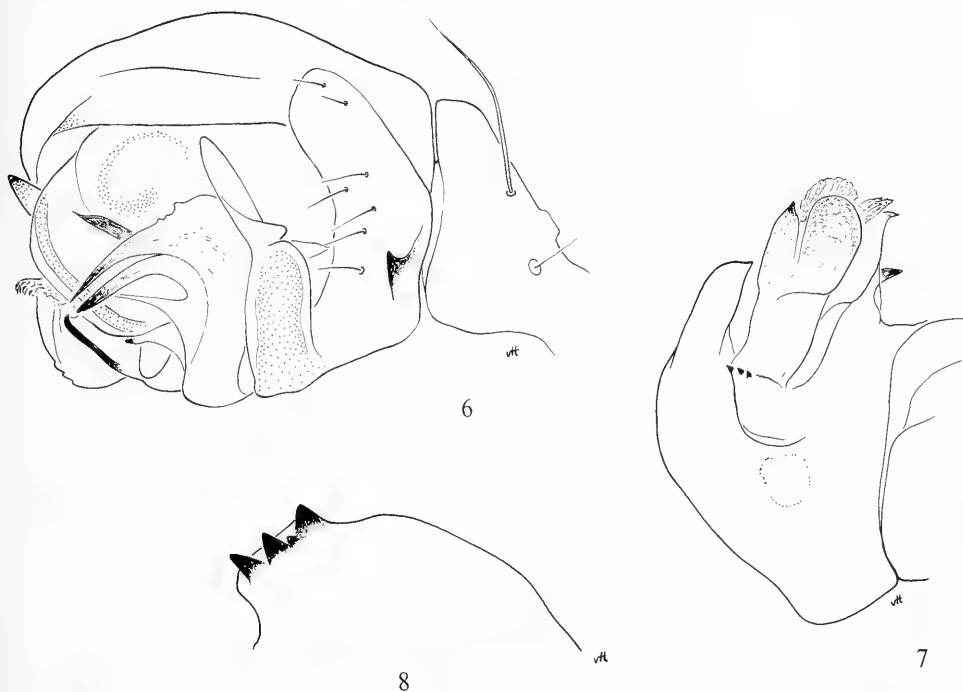


Fig. 6—8. *Lepthyphantes perseus* Van Helsdingen, spec. nov. 6, male palp, lateral aspect; 7, radical section, ventral aspect; 8, dentition on basal part of embolus, mesal aspect. 6, 7, X 200; 8, X 740

Coloration. Cephalothorax heavily suffused with grey, lateral margins and striae darkest. Chelicerae with dark grey streaks on dorsal and lateral surfaces, otherwise light brown. Sternum a shade darker, mouthparts with darker and lighter areas, as chelicerae. Legs light brown to yellow-brown, not annulated; palpal segments, the cymbium included, with strong, dark grey suffusion. Abdomen with the usual faint male pattern of cross-bars of blackish grey colour, intervening areas lighter grey with some white blotches (blotches absent in one paratype); ventral and ventro-lateral surfaces dark grey.

Chelicerae with three dorsal teeth. Stridulating files fine, as in *mengei* (Fig. 69).

Chaetotaxy of legs not differing from the generic pattern. Position of d-spine on tibia I 0.31—0.36, length of this spine 0.26—0.29 mm. Tm I 0.17—0.22.

Male palp (Fig. 6—8). Paracymbium with a single, rather obtuse, strong tooth on the posterior margin of the proximal branch. Lamella with two equally long branches, the dorsal one very gradually tapering to a slender tip, the ventral one slightly less slender and shallowly forked at its tip (when viewed from dorsal or ventral side); as in *mengei*, there is a “dorsal lobe” with a serrate margin at the point where the element curves in anterior direction. Terminal apophysis with a tongue-shaped projection which is shorter and relatively broader than in *mengei*. Basal part of embolus with three or four denticles on a projecting mesal ridge. Length of cymbium 0.27—0.29 mm.

The species is only known from the type-locality, where it was collected in a beech forest, probably in leaf-litter.

### ***Lepthyphantes flavipes* (Blackwall)**

(Fig. 9—12, 56)

*Linyphia flavipes* Blackwall, 1854: 178 (descr. ♂; England).

*Lepthyphantes flavipes*; Miller, 1947: 40, Pl. 13 Fig. 2 (♀). Locket & Millidge, 1953: 388, Fig. 231 B, D, F, 232 F (♀♂). Wiehle, 1956: 205, Fig. 344—346 (♀♂). Wanless, 1971: 23, 26, Pl. 3, Pl. 6 Fig. D (♀); 1973: 129, 134, Pl. 1 Fig. 5, Pl. 6 Fig. 5, Fig. 24B (♀).

*Lepthyphantes tenebricola*; Braun, 1960: 65 (misinterpretation of type-material of *Linyphia tenebricola* Wider signalized but again misinterpreted); 1969: 216 (idem). Braun & Rabeler, 1969: 44 (idem).

*Lepthyphantes zimmermanni*; Fage, 1931: 181 (cave record from Rumania).

*Lepthyphantes mengei*; Denis, 1952: 12 (cave record from Rumania).

*Theridium henricae* Six, 1858: 294 (descr. ♀♂; Netherlands).

Remarks. — To begin with the most disappointing discovery during our whole revisionary work in this species-group, we have to admit here that we are not convinced that figure 166 on plate 17 in Blackwall's “A History of the Spiders of Great Britain and Ireland” (part 2, 1864), where *Linyphia flavipes* Blackwall is depicted, male and female, is the same as what is now unanimously called *Lepthyphantes flavipes* (Blackwall). Especially the small figure of the male palp positively can not belong to this species. The original description of *Linyphia flavipes* by Blackwall (1854: 178) was not illustrated and the description does not help much. Original material is not available. We are not the first to suggest this discrepancy between the author's original intention and subsequent interpretation. Already Hull (1933: 106) pointed out that Blackwall's species had been misinterpreted. He also suggested (Hull & Harrison, 1937: 111) that *Linyphia flavipes*

Blackwall is the same as *Bathyphantes pullatus* (O. Pickard-Cambridge). He may be right, but we prefer to leave the case as it is, because stability is served best, at least in this case, by letting the matter rest. There is no end to *Lepthyphantes* nomenclature if we start the game of replacing well established names by others. Moreover, in most cases there is no solution to be offered with an acceptable degree of certainty.

Braun (1960) published a remark on the discrepancy between the type-material of *Linyphia tenebricola* Wider and *Lepthyphantes tenebricola* auct., though he can not be held responsible for the re-identification of the type-series. The identification of the original *tenebricola* specimens with *Lepthyphantes flavipes* (Blackwall), as stated there, was also incorrect. See also under remarks on *Lepthyphantes tenebricola* (Wider).

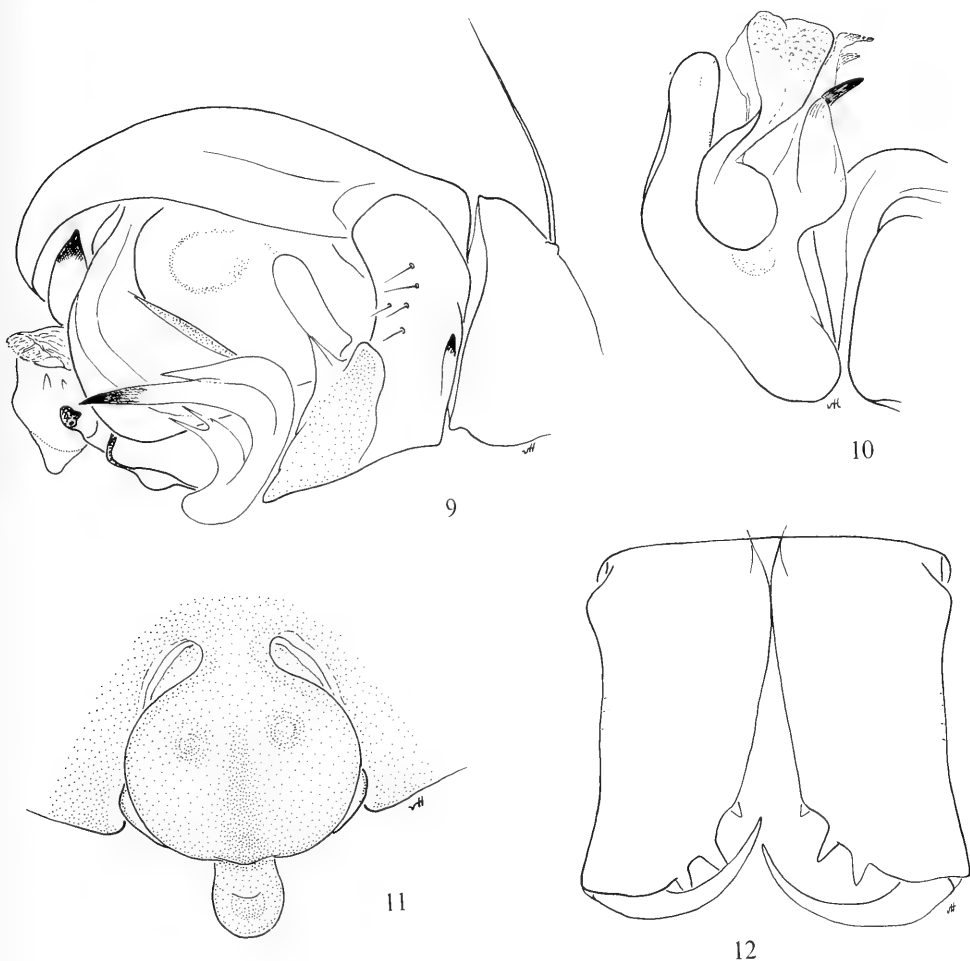


Fig. 9—12. *Lepthyphantes flavipes* (Blackwall). 9, male palp, lateral aspect; 10, radical section, ventral aspect; 11, epigyne; 12, male chelicerae, anterior aspect. 9, 10, X 200; 11, X 190; 12, X 142

The description of *Theridium henricae* by Six is very superficial and does not fit any particular Dutch species. Subsequently, the name was used, by Chyzer & Kulczyński (1894) for instance, for the species which in the British Isles was known as *Lepthyphantes flavipes* and, later again, recognized as its synonym. The question whether the name *T. henricae* was correctly applied to this species, is difficult to answer. In the Rijksmuseum van Natuurlijke Historie at Leiden there still exists a sample under this name in the Van Hasselt Collection. Van Hasselt (1885: 180) stated that he had received material of *T. henricae* from Six (type-material?), and that it was the same as *Lepthyphantes tenebricola*. (All other specimens, however, identified by him with *L. tenebricola* belong either to *Lepthyphantes tenuis* or to *L. zimmermanni*!). The sample of *T. henricae* consists of juveniles of a *Lepthyphantes* species, which indeed could be *L. flavipes*, but it is impossible to recognize the species with certainty. Besides, Chyzer & Kulczyński (1894: 69—70) maintain, that they examined two male specimens of "*Theridion Henricae*", identified by Six and kept in the collection of Thorell. From their remarks it becomes clear that this short series contained one specimen of *mengei* and one of *flavipes*.

**Diagnosis.** — *L. flavipes* is among the smallest species of the *tenuis* group. It is easily recognized by its coarse stridulating file (♀), the shape of the epigyne, and the cheliceral boss (♂). Most specimens are darkly pigmented, especially the chelicerae and the ♂ palp.

**Measurements** (in mm). Total length, ♀ 1.7—2.6, ♂ 1.7—2.2; length cephalothorax, ♀ 0.75—1.0, ♂ 0.77—0.90. Legs: Fe I 1.15—1.25 times length cephalothorax in ♀, 1.20—1.35 in ♂.

Stridulating files (Fig. 56) difficult to distinguish on the dark chelicerae (suffused with grey); widely separated ridges present in female, absent in male, or very indistinct and as widely separated as in female.<sup>1)</sup> Chelicerae of male (anterior aspect) with a latero-basal boss and concave outer surface (Fig. 12).

Male palp (Fig. 9, 10) characterized by the single, relatively sharp (cf. *mengei*) tooth on the posterior margin of the paracymbium, the shape of the lamella (with the terminal branches standing about perpendicular on the subterminal part), and the absence of denticles on the basal part of the embolus. The tooth on the paracymbium is situated slightly more to the dorsal side than in *mengei*. The terminal part of the embolus has a characteristic lobe-like extension on the latero-ventral side (lateral aspect). The basal segments of the palp are strongly suffused with grey, as are the chelicerae. Length of cymbium 0.27—0.30 mm.

Epigyne (Fig. 11) easily distinguished from that of the other species of this group by the characteristically rounded basal part of the scape. Posterior median plate hardly visible in the ventral aspect. There are two lateral depressions on the basal part of the scape, but these are often very slight and hardly visible. Width of scape 0.140—0.175 mm.

<sup>1)</sup> This has already been pointed out in an earlier paper (Van Helsdingen, 1963: 36, Fig. 5, 6), but by mistake the figure of the male chelicerae (Fig. 6) was said to be the female, and vice-versa.

Distribution. — According to Bonnet, the species is restricted to Central Europe, including the British Isles; up to 1940 it was stated not to have been recorded from Scandinavia north of Denmark (see, however, remarks below), from Poland, the southern Balkans, or from Portugal. Since 1940 it has been found in southern Finland, Poland, the European U.S.S.R., and Italy (cave).

It has been mentioned from caves in Hungary (Boker, 1922; Kolosváry, 1928) Switzerland (Dresco, 1960, entrance), Italy (Brignoli, 1971), Spain (Fage, 1931), and also occurs in caves in Rumania (Fage, 1931: 181, sub *zimmermanni*; Denis, 1952: 12, sub *mengei*; both re-examined, MP). See also Wolf (1934—1937).

We have examined material from Austria (North Tirol, common), Czechoslovakia (Böhmen, common), Yugoslavia (Slovenia, Hercegovina), Rumania (material recorded by Niculescu, 1968), Italy (southern Alps, Parma, and Piemonte), Spain (Prov. Huesca, Rodellar, leg. E. Duffey), and Holland (common). The figures are based on specimens from Holland.

The following material has been re-examined: cave records from Spain by Fage (1931) from the provinces Tarragona and Soria (MP); cave records from Rumania by Denis (1952: 12, sub *mengei*; MP) and by Fage (1931: 181, sub *zimmermanni*; MP); identified material in the Muséum National d'Histoire Naturelle, Paris.

Through the kindness of Dr. T. Kronstedt of the Naturhistoriska Riksmuseet, Stockholm, a number of specimens could be examined, which are labelled "*Linyphia pygmaea* Sundevall" and are part of the Westring collection. Among the seven specimens examined, four were found to belong to *flavipes*. Westring's specimens are assumed to originate from Sweden, probably from the surroundings of Göteborg, and thus we may have found an early proof of the existence of *L. flavipes* in southern Sweden. It should be pointed out here that Chyzer & Kulczyński (1894: 70) were already aware of the existence of *L. flavipes* ("*L. Henricae*") in Sweden. They reported to have seen specimens of this species in the collection of Thorell, partly under the name of *Linyphia pygmaea* (!). Bonnet appears to have overlooked this important remark.

Thus *L. flavipes* appears to be indeed a Central European species, reaching its northern limit in Great-Britain, Holland, Denmark, southern Sweden, southern Finland, Poland and the European U.S.S.R.<sup>1)</sup> The upper limit in the Alps lies at about 1200 m; in the Apennines there is a record from 1650 m (Parma). The southern slopes of the Pyrenees, the Apennines, Slovenia, and Bulgaria form the southern limit of its distribution, apart from the Spanish cave records from Tarragona and Soria still more to the south.

It is a typical leaf-litter inhabiting species, in deciduous as well as coniferous forests. Adults throughout the whole year (Braun & Rabeler, 1969: 44, sub *tenebricola*).

<sup>1)</sup> There is a cryptic remark by Palmgren (1972: 91), who states to have found specimens of *Lepthyphantes zebrinus* (Menge) in southern Finland, suggesting at the same time that this probably is a geographical race (subspecies) of *Lepthyphantes flavipes*. This is the more surprising since Moritz (1968) redescribed *L. zebrinus* and demonstrated a number of apparent differences between the two species. In *zebrinus* the stridulating files are much finer, the epigyne has a medially excised scape, the paracymbium of the male palp is toothless and of quite different shape, and the lamella does not show any resemblance with that of *flavipes*. In our opinion *zebrinus* belongs to a different species-group.

**Lepthyphantes herbicola Simon**  
(Fig. 13-15, 57)

*Lepthyphantes herbicola* Simon, 1884: 323, Fig. 92 (descr. ♀ ♂ ; France: Var, Alpes-Maritimes, Corse); 1929: 590, 595, Fig. 900-901 (♂ ♀, diagnosis), 733 (references). De Dalmas, 1922: 88 (France: Ile Giglio; cat.). Denis, 1933a: 572 (Pyrénées-Orientales); 1933b: 95 (Var); 1934: 152 (Var); 1935: 121 (Var); 1949: 18 (Provence).

Remarks. — It is not clear whether the original material of Simon is still extant. The species was described in 1884 from the Départements Var, Alpes-Maritimes and Corse. In the Paris Museum the available material from the time of Simon is labelled Marseille and Banyuls, while there is also one series without a locality label. A lectotype thus cannot be selected. There is no need for a neotype because the species is not easily confounded with any of its congeners.

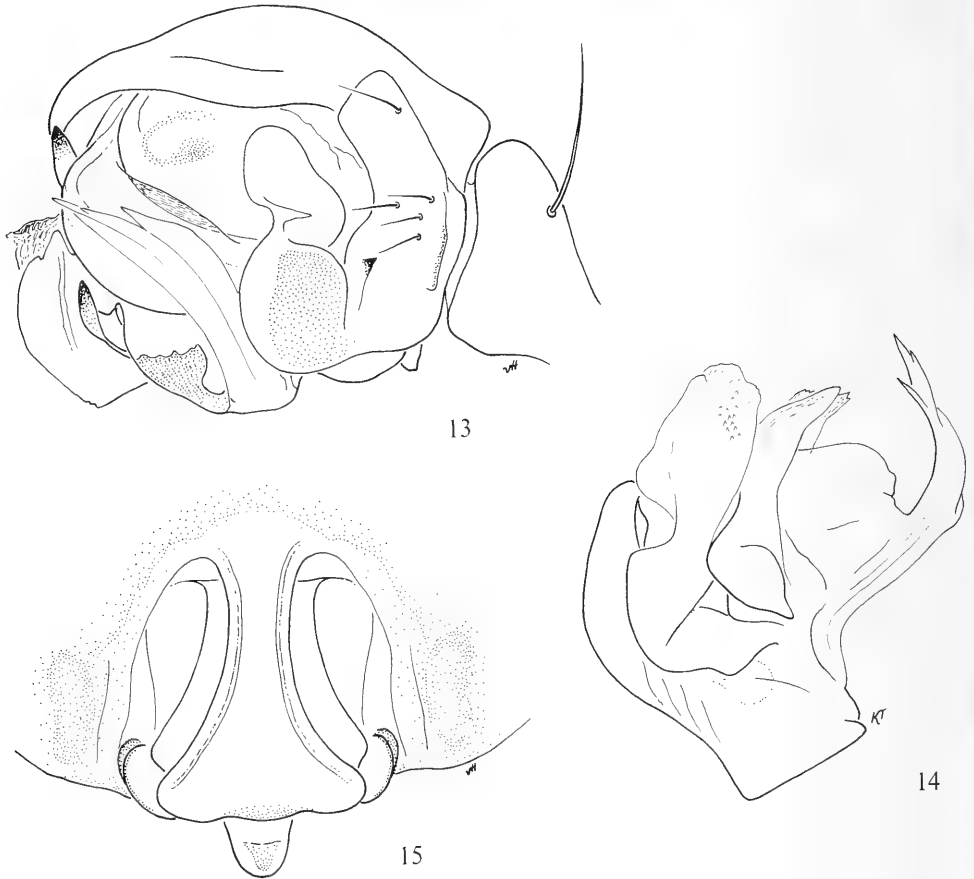


Fig. 13—15. *Lepthyphantes herbicola* Simon. 13, male palp, lateral aspect; 14, radical section, ventral aspect; 15, epigyne. 13, 15, X 200; 14, X 180

Diagnosis. — *L. herbicola* belongs to the smaller species of the group and is well characterized by its genitalia.  
Measurements (mm). Total length, ♀ 1.8-2.3, ♂ 1.7-2.1; length cephalothorax,



♀ 0.77-0.92, ♂ 0.76-0.92. Legs: Fe I 1.1-1.3 times length cephalothorax in females, 1.15-1.30 times in males.

Stridulating files rather fine (Fig. 57), slightly coarser than in *mengei*.

Male palp (Fig. 13, 14) with only one small tooth on the paracymbium at the anterior margin of the proximal branch (in contradistinction to *mengei* and *flavipes*); the distal branch is much less slender than in the other species of the group and appears to be rather strongly pigmented. The lamella is only slightly curved and shows the usual dorsal and ventral arms. Embolus without denticles on basal part. Length of cymbium 0.29-0.33 mm.

Epigyne (Fig. 15). Scape with gradually widening basal part with concave margins; inner scape equally wide as basal part and also with concave margins; posterior median plate distinct in the ventral aspect. As the specimens themselves, the epigyne is small. Width of scape 0.125-0.150, of inner scape 0.125-0.140, of posterior median plate 0.160-0.190 mm.

Distribution. — Literature records all refer to southern France and Corse; on the mainland the species is restricted to the following provinces: Pyrénées-Orientales, Bouches-du-Rhône, Vaucluse, Var, Alpes-Maritimes, and Drôme. In 1934, Denis stated it to be not uncommon ("Assez fréquent, sous les pierres et dans les mousses") and Simon, too, indicates it to be common near Menton (1929). Other samples come from moss and litter in mixed or coniferous forest.

We have studied all available identified material in the collection of the Paris Museum (from Marseille, Banyuls, and an unlabelled series). New records can be given here from:

France: Ardèche, Planzoles W. of Joyeuse, 700 m, open pine forest, 18.vii.1974, P. J. van Helsdingen, 1♀ 1♂; W. of Joyeuse, mixed pine-chestnut forest, 7.vii.1974, P. J. van Helsdingen, 1♀ (both ML).

Italy: Naples, 1♀ 2♂, MP; Portici near Naples, 1♂, MP; Portici, 6♀, MP; Isola Ischia near Naples, 1♀ 1♂, Mus. Bergamo.

Algeria: Edough, 5♀ 1♂, MP.

Spain: Prov. Huesca, Rodellar, 8.vi.1973, sifted from moss in gorge near Rio Mascùn, leg. E. Duffey and in his collection, 4♀ 2♂.

Yugoslavia: Dalmatia, Spilja Vranjača, Kotlenice n. Split, 5.viii.1971, 1♂; Isl. Cres, Lipica jama, 1♀; both leg. C. Deeleman, ML.

All figures were made after specimens from Marseille.

### ***Lepthyphantes tenuis* (Blackwall)**

(Fig. 16-18, 58)

*Linyphia tenuis* Blackwall, 1852: 18 (nom. nov. pro *Linyphia pusilla* Blackwall, preoccupied by *Linyphia pusilla* Sundevall [= *Microlinyphia pusilla* (Sundevall)]).

*Lepthyphantes tenuis*; Locket & Millidge, 1953: 385, Fig. 230 E, 232 A (♀ ♂). Wiehle, 1956: 197, Fig. 331-335 (♀ ♂). Wanless, 1971: 22, 26, Pl. 2 Fig. A, B, Pl. 6 Fig. A (♀); 1973: 129, 132, 134, Pl. 1 Fig. 1, Pl. 4 Fig. 7, Pl. 6 Fig. 1 (♀).

*Lepthyphantes falteronensis* Di Caporiacco, 1936: 350 (descr. ♀ ♂; Italy, Apennines). **Syn. nov.**

*Lepthyphantes aspromontis* Di Caporiacco, 1949: 133, Fig. p. 134 (descr. ♂; Italy). Alberti, 1967: 26 (type catal. Mus. Triest). **Syn. nov.**

*Lepthyphantes sanfilippoi* Di Caporiacco, 1950: 108, Fig. 2 (descr. ♂; Italy, Liguria, in cave). **Syn. nov.**  
? *Linyphia arctica* Keyserling, 1886: 85, Pl. 14 Fig. 179 (descr. ♀; Sitka, Alaska).  
*Lepthyphantes zimmermanni*; Fage, 1931: 181 (Portugal, cave).

Remarks. — The name *tenuis* was introduced by Blackwall as a replacement name for his *pusilla* in the genus *Linyphia*, which name had already been used in this genus as a primary combination by Sundevall. We have not located any original material of Blackwall's *Linyphia pusilla*.

The original material of *Lepthyphantes falteronensis* Di Caporiacco could be located in the collection of Di Caporiacco in the Museo Zoologico in Firenze (MZF). It consists of 2 ♂ from Falterona and 2 ♂ from Monte Acuto. Not all specimens are in good condition: from either locality one specimen lacks both palps, the second specimen from Monte Acuto has a left palp only, the material from Monte Falterona is accompanied by a loose palp. The only complete specimen (from Monte Falterona) is designated lectotype here. The type-locality, Monte Falterona, is situated ENE of Florence in the Apennines. The specimens were collected at 1650 m (Mt. Falterona) and 1428 m (Mt. Acuto), respectively.

The male holotype of *Lepthyphantes aspromontis* Di Caporiacco, described from Italy (Calabria, Aspromonte), could be examined through courtesy of Dr. G. Alberti of the Museo Civico di Storia Naturale at Trieste, where the type is preserved. It belongs to *L. tenuis* (Blackwall).

Of the original material of *Lepthyphantes sanfilippoi* Di Caporiacco only one specimen could be located. It is selected as the (male) lectotype here. It is preserved at the Museo Civico di Storia Naturale at Milano and could be examined through the kindness of Dr. C. Leonardi. It appears to belong to *Lepthyphantes tenuis* (Blackwall).

The original material of *Linyphia arctica* Keyserling (1 ♀ only?) could not be located at the AMNH, nor at the BM; it is probably lost. Our suggestion of a possible synonymy is mainly based on the small figure of the epigyne while measurements and other details given by Keyserling agree with *tenuis*.

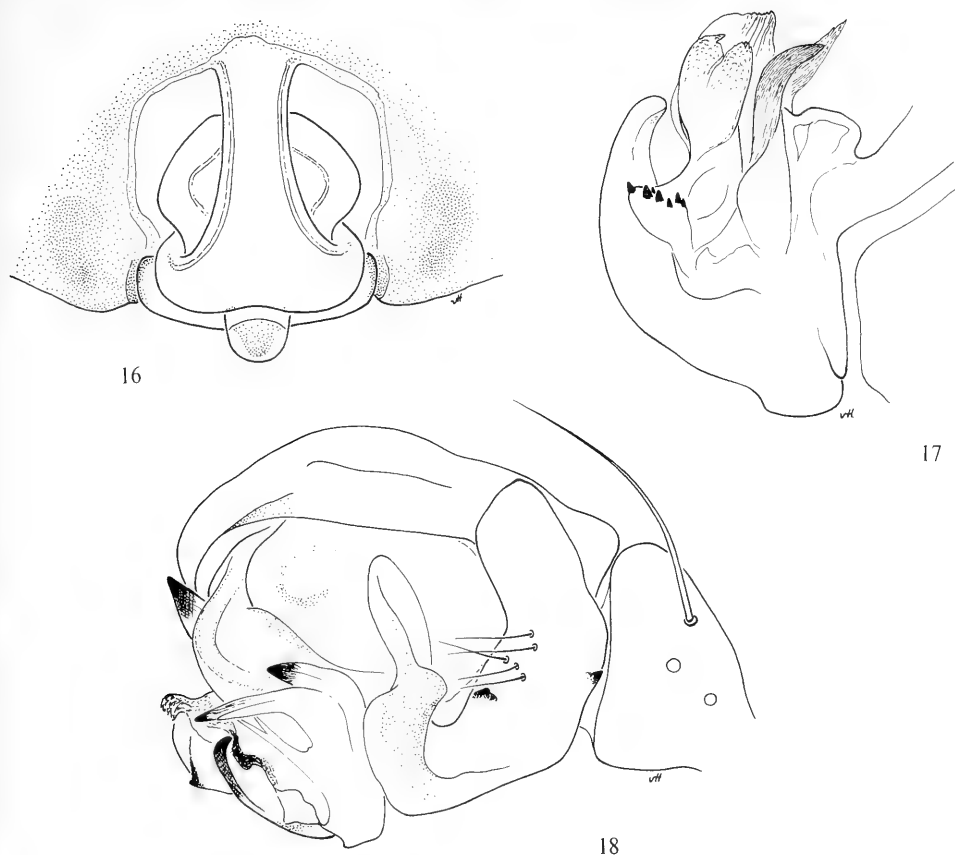
Specimens from la Palma, Canary Islands, are said to be different from the normal form in the shape of the lamella, the dentition of the paracymbium, and the coloration (Schmidt, 1975b). We have not seen the specimens.

Diagnosis. — A comparatively light species of small size. The paracymbium has a very characteristic pair of denticles, the lamella is easily recognized by its shape, the scape of the epigyne has the shape of an anchor.

Measurements (in mm). Total length, ♀ 2.3-2.8, ♂ 1.95-2.4; length cephalothorax, ♀ 0.95-1.10, ♂ 0.82-1.02. Legs: Fe I 1.25-1.35 times length cephalothorax in females, 1.25-1.4 times in males.

Stridulating files rather coarse (Fig. 58).

Male palp (Fig. 17, 18) easily recognized by the dentition of the paracymbium and the rather blunt dorsal branch of the lamella. Paracymbium with a small and sharp denticle at the posterior margin and a second, barely larger and slightly more conical denticle at the anterior margin of the proximal branch; posterior denticle pointing outward and backward, more outward than in *zimmermanni*. Lamella relatively small, the dorsal branch ending well before ventral branch, with



16

17

18

Fig. 16—18. *Lepthyphantes tenuis* (Blackwall). 16, epigyne; 17, radical section, ventral aspect; 18, male palp, lateral aspect. 16, X 194; 17, 18, X 180

obtuse tip; ventral branch slender and rather straight, sometimes forked at tip. Embolus with well-developed cluster of small teeth on basal part, numbering at least 7. Length of cymbium 0.29-0.34 mm.

Epigyne (Fig. 16) with a distinctly anchor-shaped scape; anterior section more or less parallel-sided or with concave margins, gradually diverging in posterior direction but not fluently passing into margins of broadest part of visible scape; inner scape with conspicuously rounded lateral lobes, about as wide as broadest point of exposed scape; posterior median plate hardly wider than scape. Width of scape 0.135-0.165, of inner scape 0.125-0.150, of posterior median plate 0.160-0.190 mm.

<sup>1</sup>) It has been suggested by Simon (1929: 733, footnote 2) that *Linyphia* (*Lepthyphantes*) *taczanowskii* O. P.-Cambridge, 1873 [misprinted *tarzanowskii*] would be close to *tenuis*. However, re-examination of the original material, which is still preserved in the collections of the Hope Department of Zoology (Entomology) at Oxford, revealed it to be a senior synonym [**syn. nov.**] of *Lepthyphantes trucidans* (L. Koch, 1879), described from the Yenisey region in Siberia. *Linyphia taczanowskii* was also collected in Siberia (Lake Baikal). *L. trucidans* does not fit in with the *tenuis* group.

Distribution. — For *Lepthyphantes tenuis*, Bonnet listed references for nearly all European countries with the exception of Iceland, Norway, Sweden and Finland. Russia and the Caucasus<sup>1)</sup> formed the eastern limit, Greece, Italy, Spain and Portugal the southern limit on the European mainland. Several records were available from the Açores, Madeira and New Zealand, but none from mediterranean North Africa.

Since 1940, this distribution was confirmed for many countries, while new countries could be added to it: Afghanistan (Denis, 1958) and Finland (Prov. Vaasa, 63°N, Hackman, 1951; Tvärminne, southern Finland, Palmgren, 1972, 1975). The occurrence of this species in the Canary Islands was established by Schmidt (1975 a, b), the occurrence on Madeira and the Açores was confirmed by Denis (1962 a and 1963, and 1964, respectively). Recently (Bragg & Leech, 1972) it has been recorded also from the Nearctic region (British Columbia, ♀ only), from where it probably had been recorded already by Keyserling (1886).

The species has been found in caves in Belgium (Leruth, 1935, 1939), France (Denis, 1959: Pyrenees), Portugal (Fage, 1931: sub *zimmermanni*, re-examined), Italy (Brignoli, 1971), and Bulgaria (Drensky, 1931; Deltshev, 1972 a, 1972 b, 1973). See also Wolf (1934-1937).

Samples have been re-examined from the Açores (Berland, 1932), New Zealand (De Dalmas, 1917), and Portugal (Fage, 1931: 181, *zimmermanni* 1♂, belongs to *tenuis*) (all MP).

Material has been found from the following countries, so that the known range can be extended to: Algeria (several series from Edough, Constantine and Sétif; MP), Lebanon (MP), Norway (Bergen; MP).

The diagnosis, measurements and figures are based on material from Holland (common), France (Menton), Czechoslovakia (not uncommon, lowland), Bulgaria (cave), and Italy (type-series of *L. falteronensis* and *L. aspromontis*). Specimens from Greece (Salonique, MP) and Spain (Prov. Huesca, Rodellar; BM) were also used.

With records from Madeira, the Canary Islands, Algeria, the Lebanon, and Afghanistan, *L. tenuis* reaches further south and south-east into warm, subtropical regions than most members of the *tenuis* group. It does not occur far to the north and appears to be rare there. In the Alps it is restricted to lower altitudes.

In New Zealand it must have been introduced. At least this is the only reasonable explanation for the extremely wide gap in the distribution. According to R. R. Forster (in litt.) it is extremely common in open country and in and around gardens in settled areas, but it does not occur in native forests. It also seems to be spreading to other islands in the south. For the Nearctic region an introduction is less self-evident. Recently 3 ♀ have been mentioned from W. Canada (Bragg & Leech, 1972, British Columbia), while we (vH) also received for examination a ♀ specimen from the State of Washington, through the kindness of Dr. Dondale, Ottawa. If *Linyphia arctica* Keyserling is indeed based on a specimen of *tenuis*, as suggested above, the species has been found also in southern Alaska (Sitka). Importation of spiders by man in the Nearctic Region is reported on by Lindroth (1957), on the east as well as on the west coast. However, we should be very careful with hasty conclusions.

*L. tenuis* does occur in the litter stratum in forests, but it is equally common in a wide variety of other habitats. In Holland it is, among other habitats, very common in tussocks of Marram grass on the seadunes. Adults throughout most of the year (Braun & Rabeler, 1969: 44).

***Lepthyphantes tenebricoloides* Schenkel**

(Fig. 19-21, 59)

*Lepthyphantes tenebricoloides* Schenkel, 1938: 15, Fig. 5 a-e (descr. ♀ ♂; Madeira). Denis, 1941: 113 (Tenerife); 1962 a: 77 (Madeira). Forcart, 1961: 72 (catalog.). Schmidt, 1975 a: 224 (Canary Islands; aberrant specimens?); 1975 b: 235 (Canary Islands).

Remarks. — The original description by Schenkel is lengthy and detailed and includes remarks on the variation in abdominal patterns. The original material should be at the Naturhistoriska Riksmuseet at Stockholm. We have only seen 3 ♀ and 3 ♂ paratypes from the Schenkel collection at Basel (not 2 ♀ and 4 ♂ as stated by Forcart, 1961: 72).

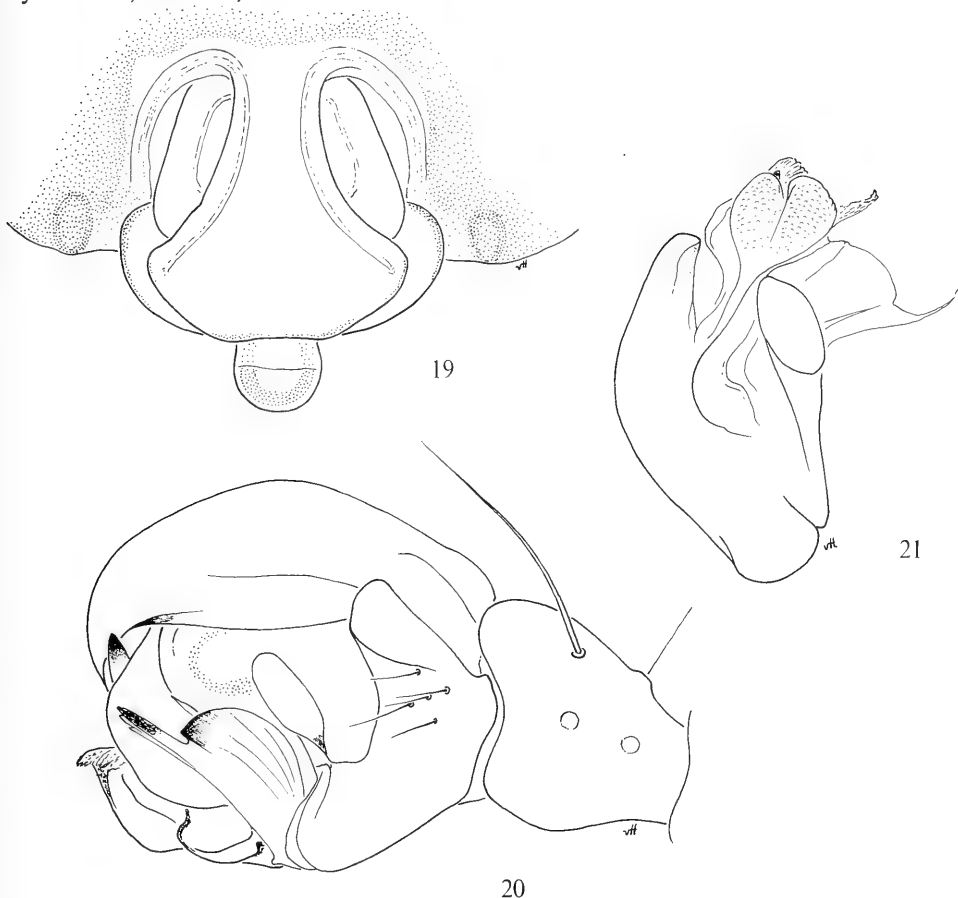


Fig. 19—21. *Lepthyphantes tenebricoloides* Schenkel. 19, epigyne; 20, male palp, lateral aspect; 21, radical section, ventral aspect. 19, X 190; 20, 21, X 160

According to Schmidt (1975 a), recently collected material from Gomera, Canary Islands, differs considerably from the description by Schenkel, especially as to the paracymbium. In the Madeira specimens the paracymbium is toothless; those from Gomera are said to show some dentition, but the position of the teeth is not indicated.

Diagnosis. — *L. tenebricoloides* is very light: the cephalothorax a very light yellow-brown with a narrow median dark grey streak that widens to the breadth of the eye-region in front; the abdomen gives a light impression and bears pairs of black spots dorsally, though the darker parts can be more pronounced in some specimens (see Schenkel's description and figures). On the ventral surface of the abdomen there are a pair of latero-ventral light spots halfway between the epigastric furrow and the spinnerets.

Measurements (in mm). Total length, ♀ 2.6-4.1, ♂ 2.6-3.0; length cephalothorax, ♀ 1.2-1.55 (Schenkel mentioned a female cephalothorax length of 1.7), ♂ 1.2-1.37. Legs: Fe I 1.1-1.2 times length cephalothorax in females, 1.2-1.35 times in males.

Stridulating files (Fig. 59) rather fine, conspicuous and well-developed in the males, less conspicuous in the females. Dorsal margin of chelicerae with three teeth as usual, but teeth long and slender, distinctly longer than in other species of this group.

Male palp (Fig. 20, 21). Paracymbium without any teeth. Lamella with a nearly straight ventral margin, the ventral branch projecting straight forward and slightly dorsal, the dorsal branch rounded-truncated. Base of embolus without denticles. Length of cymbium 0.35-0.39 mm.

Epigyne (Fig. 19) with basal part of scape gradually widening with concave margins towards broadest point; lateral lobes of inner scape as wide as basal part, their lateral margins about straight and converging in anterior direction; posterior median plate slightly wider than scape. Width of basal part of scape 0.150-0.200, of inner scape 0.160-0.175, of posterior median plate 0.185-0.225 mm.

Distribution. — *L. tenebricoloides* was described from Madeira. It has also been recorded from the Canary Islands (Denis, 1941). There are no records outside this archipelago. Recently again recorded from the Canary Islands (Schmidt, 1975 a, b), but the specimens are reported to disagree with the original description.

**Lepthyphantes drenskyi** Van Helsdingen, spec. nov.  
(Fig. 22, 23, 60)

One sample of this new species was found in what is left of Drensky's collection in the Zoologisches Institut der Bulgarischen Akademie der Wissenschaften, Sofia; it had been identified (by Drensky?) with *L. tenebricola*. However, it appears to be different from *tenebricola* and rather reminds of *tenuis*, from which it differs in the dentition of the paracymbium, the number of denticles on the embolus, and the stridulating files. There are no adult females in the sample.

Types. — ♂ holotype from Dragalewzi near Sofia, vi.1909, P. Drensky.

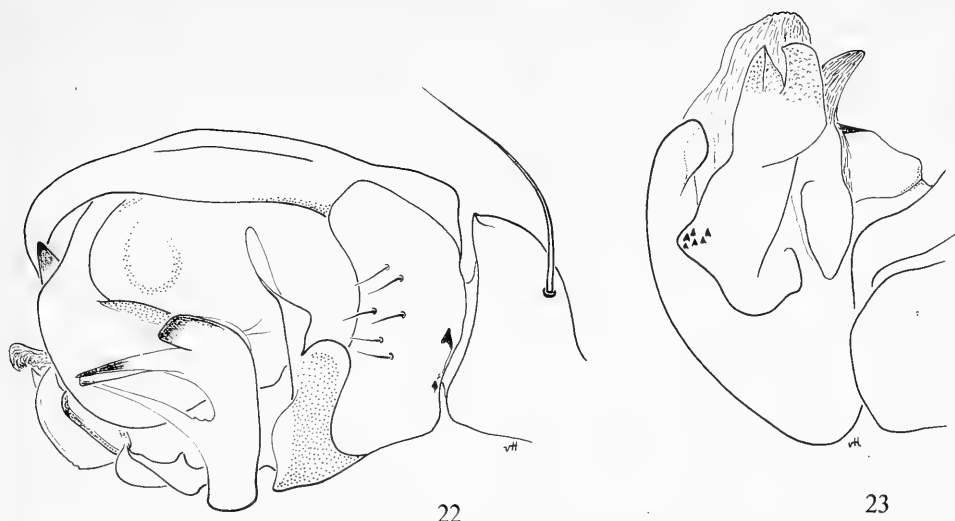


Fig. 22—23. *Lepthyphantes dremskyi* Van Helsdingen, spec. nov. 22, male palp, lateral aspect; 23, radical section, ventral aspect. X 142

Paratypes (1♂, 1 subadult ♂, 1 subadult ♀) from the same locality, preserved with the holotype. All specimens are in the Zoologisches Institut at Sofia.

**Description.** — Measurements (in mm). Male. Total length 2.2-2.4, length cephalothorax 0.95-1.05. Fe I 1.25-1.40 times length cephalothorax.

**Coloration.** The specimens are light yellow-brown (discoloured through preservation?). Dorsal pattern distinct, composed of greyish chevrons.

Chelicerae with coarse stridulating files (Fig. 60). Legs with the usual spines, position of the retrodorsal (basal) spine on tibia I 0.30-0.31, length of this spine 0.325 mm. Tm I 0.22. palp (Fig. 22, 23). Paracymbium with a single, small denticle at posterior margin. Embolus with four denticles on the protruding part of the basal half. Lamella not unlike that of *tenuis*, but the dorsal branch more truncate, blunt, not pointed. Length of cymbium 0.38-0.40 mm.

As indicated above, *L. dremskyi* is not unlike *tenuis*, but in that species the paracymbium bears a second tooth at the anterior margin of the proximal branch, the embolus has seven or more teeth, and the dorsal branch of the lamella is short, but distinctly pointed, not truncate. The stridulating files make a coarser appearance.

The species is named after Pentcho Drensky, as a late homage to this well-known Bulgarian arachnologist, who has contributed so much to our knowledge of the Bulgarian spider fauna, and who also collected the type-series.

### ***Lepthyphantes zimmermanni* Bertkau**

(Fig. 24-27, 61)

*Lepthyphantes zimmermanni* Bertkau, 1890: 10 (nom. nov. pro *Lepthyphantes zebrinus* Simon, 1884). Locket & Millidge, 1953: 386, Fig. 230 B, C, 231 G, 232 B (♀♂). Wiehle, 1956: 200, Fig. 336-339 (♀♂). Wanless, 1971: 22, 26, Pl. 2, Pl. 6 Fig. B (♀); 1973: 129, 134, Pl. 1 Fig. 4, Pl. 6 Fig. 4 (♀).

*Lepthyphantes borealis* Braendegård, 1932: 12, Fig. 2 (descr. ♀; Iceland); 1958: 84, 85 (= variety of *zimmermanni*).

*Lepthyphantes cristatus*; Simon, 1892: clxxvii (Iceland).

Remarks. — Simon (1929: 595) described a variety *spiniger* from Southern France, which subsequently has been recognized as a separate species (Dresco & Jézéquel, 1961). It is treated as such in this paper.

Diagnosis. — The male of this species is well characterized, apart from the shape of the lamella, by the peculiar small and sharp backward pointing denticle

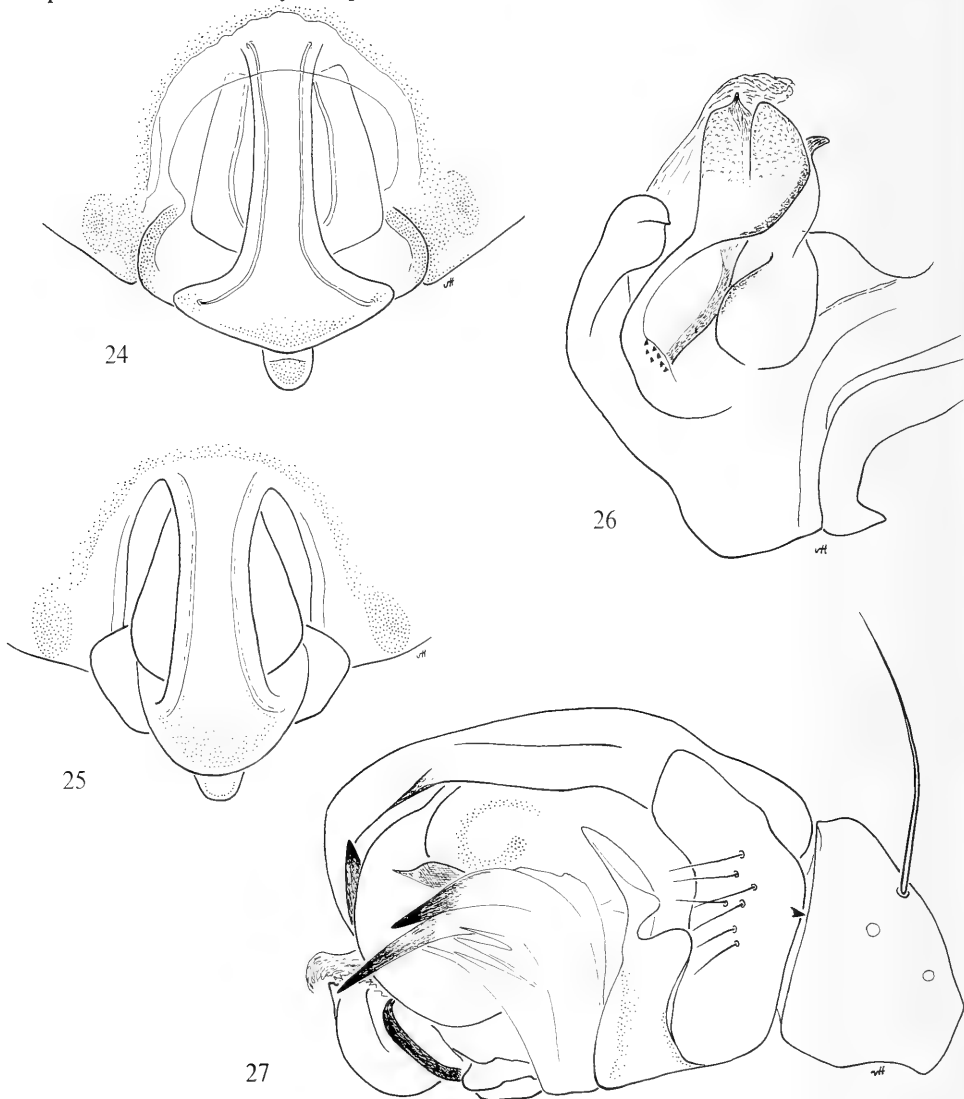


Fig. 24—27. *Lepthyphantes zimmermanni* Bertkau. 24, epigyne (specimen from Holland); 25, epigyne (specimen from Bulgaria); 26, radical section, ventral aspect; 27, male palp, lateral aspect. 24, X 165; 26, 27, X 160; 25, X 142



on the posterior margin of the paracymbium. The epigyne is much like that of *L. floriana*, but there are differences in the shape of the scape and the laterally protruding wings of the underlying arched part of the latter species.

Measurements (in mm). Total length, ♀ 2.2-3.1, ♂ 2.2-2.75; length cephalothorax, ♀ 0.95-1.25, ♂ 1.0-1.25. Legs: Fe I 1.2-1.4 times length cephalothorax in females, 1.15-1.35 times in males.

Stridulating files (Fig. 61) coarse at base to rather fine toward apex, well-developed, slightly coarser than in *floriana* from Rumania.

Male palp (fig. 26, 27) characterized by the single small but sharp tooth near the posterior margin of the paracymbium, which points backward rather than outward. Lamella evenly curved, with a distinct separate dorsal branch and a much longer ventral branch, the latter slender and tapering to a sharp tip. Base of embolus on ventral side with seven denticles (cf. *spiniger*). Length of cymbium 0.37-0.43 mm.

Epigyne (Fig. 24) with a long and slender anterior section of basal part of scape, parallel-sided, rather suddenly widening into the much broader posterior section; lateral wings of inner scape rather angular, margins in front of projecting angle rather straight; inner scape as wide as basal part; posterior median plate distinctly wider than scape (shape of median plate much depending on angle of vision). Width of basal part of scape 0.150-0.175, of inner scape 0.150-0.175, of posterior median plate in ventral view 0.210-0.250 mm.

Morphological variation. A slightly aberrant specimen from Bulgaria (♀, Fig. 25) is tentatively placed here, though the ventral aspect of the scape is obviously different; also the posterior aspect reveals a swollen ventral surface of the basal part of the scape, while this part is much flatter in *zimmermanni*. It is unfortunate that we do not have any *zimmermanni* male from Bulgaria, or a good sample of this type of female with matching males.

Distribution. — The records up to 1940, as given by Bonnet, cover most of Europe, including the British Isles but with the exception of Norway, Sweden and Finland, Poland and more to the east. There are, however, records from the Faroers, and also from Iceland, where it seems well-established (Braendegård, 1958: 85). In Southern Europe there are records from Portugal (Fage, 1931: 181: = *tenuis*, re-examined), from Spain (Galiano, 1910, sub *zebrinus*, citing a record by Simon; Denis, 1938; Fage, 1931, cave record, re-examined), and from Italy (several authors). The Balkans and Hungary formed the eastern boundary in 1940. The original description of *Bathyphantes pygmaeus* Menge is considered by some authors to refer, at least partly, to *zimmermanni*; in that case Poland (Danzig) falls within the distribution of the species as known up to 1940.

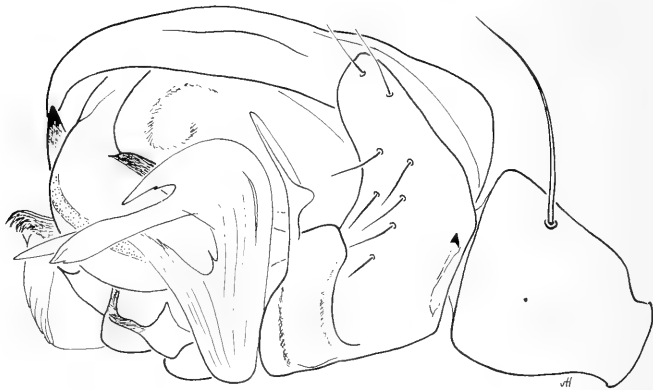
Since 1940, there are new records, among others, from Poland, European U.S.S.R., Bulgaria, Finland and Ireland. There is one record from northern Yugoslavia (Polenec, 1958).

Cave records come from Belgium (Leruth, 1935, 1939), France (Fage, 1931, re-examined; Denis, 1959, Pyrenees; Denis, 1967, Haute-Garonne), from Spain (Fage, 1931, re-examined), Bulgaria (Deltshev, 1972 a, 1972 b, and 1973; specimen re-examined and identification maintained, despite observed differences (Fig. 25)).

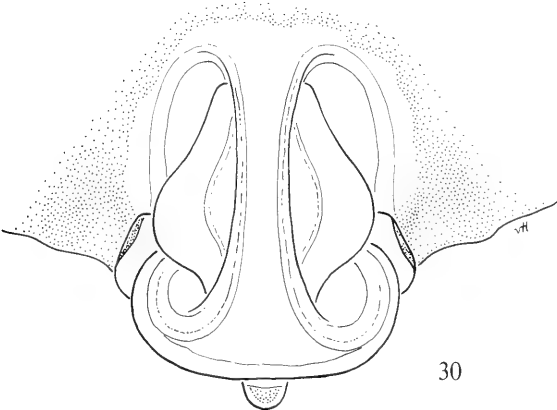
The cave records from Portugal (Fage, 1931: 181, = *tenuis*, re-examined) were based on misidentifications. See also Wolf (1934-1937).

We have examined a fair number of specimens from Switzerland (coll. Schenkel) and France (coll. Simon). A specimen in the collection of Simon, originating from Iceland and identified with *L. cristatus* (Menge) (Simon, 1892 ?), was found to belong to *zimmermanni*. Other examined material came from Czechoslovakia (one locality only), Bulgaria (1 ♀ only, in cave), and Holland. In Tirol and eastern Switzerland it seems to be lacking. The distribution in the Balkans is hardly known. We presume *zimmermanni* to be absent from higher mountainous regions. Our figures are based on specimens from Holland.

*L. zimmermanni* is found in the litter stratum of preferably coniferous forest (Braun & Rabeler, 1969: 44).



28



30



29

Fig. 28—30. *Lepthyphantes spiniger* Simon. 28, male palp, lateral aspect; 29, radical section, ventral aspect; 30, epigyne. 28, 29, X 160; 30, X 200

***Lepthyphantes spiniger* Simon**  
(Fig. 28-30, 62)

*Lepthyphantes zimmermanni spiniger* Simon, 1929: 595 (descr.; Pyrenees and Alps), 733 (reference). Fage, 1931: 181, 237 (France: cave in Ariège). Dresco, 1949: 187 (France: Pyrénées-Centrales). Denis, 1957: 254 (Pyrénées).

*Lepthyphantes spiniger*; Dresco & Jézéquel, 1961: 105, Fig. 1-4 (descr. ♂ ♀, distinct species; Basses-Pyrénées, Hautes-Pyrénées, Haute-Garonne).

**Remarks.** — The collection of the Muséum National d'Histoire Naturelle at Paris contains a number of samples of this species, but it is not clear which of these belongs to the material on which Simon based his diagnostic remarks. All samples contained specimens of other species as well. Still we do not think it necessary to select a lectotype, because the species is quite characteristic and can hardly be confounded with any of the group members.

**Diagnosis.** — *L. spiniger* is most easily distinguished from its congeners by the spinose metatarsi and the very fine stridulating files of the chelicerae.

**Measurements (mm).** Total length, ♀ 2.7-3.2, ♂ 2.1-2.7; length cephalothorax, ♀ 1.10-1.27, ♂ 1.10-1.20. Legs: Fe I 1.15-1.3 times length cephalothorax in females, 1.25-1.45 times in males.

Stridulating files (Fig. 62) very fine in both sexes. Metatarsi with a l'- and l''-spine beside the usual dorsal spine, but metatarsus III not always bearing a complete set.

Male palp (Fig. 28, 29) characterized by the large lamella, which has the longer terminal branch forked, and by the large number of denticles (11) on the basal part of the embolus. The paracymbium bears a single small tooth, which does not point backward as in *zimmermanni* but dorsad, while below it a ridge-like excrescence is found along the posterior margin. Length of cymbium 0.36-0.41 mm.

Epigyne (Fig. 30) resembling that of *zimmermanni*, but posterior section of basal part of scape more clearly showing the reversal of its course, the lateral margins distinctly curving anterad; lateral wings of inner scape wide and broadly rounded; entire scape slightly more protruding posterad. Posterior median plate less visible than in *zimmermanni*. Width of basal part of scape 0.150-0.190, of inner scape (measured between apices of wings) 0.160-0.175, of posterior median plate 0.185-0.225 mm.

**Distribution.** — The species, according to Simon, 1929 (p. 733), occurs in coniferous forests in the Pyrenees and the Alps. Actually this can only be confirmed for the Pyrenees. We have examined all available material at the Muséum National d'Histoire Naturelle at Paris, which came from Bagnères-de-Bigorre (Hautes-Pyrénées), from the "Basses-Pyrénées", from the Grotte d'Aubert (Ariège: Moulis), and from the Grotte de Lestelas (Ariège: St. Lizier) (Fage, 1931). Apart from Simon's reference to the Alps, all other authors gave records from the Pyrenees only. Of four tubes in the Paris Museum the labels bear only numbers, which appear to be of no help in establishing the origin of the material. These samples might indeed come from the Alps, but we should like to have confirmed the occurrence in this region by fresh and well-localized captures.

Nearly all samples referred to above were a mixture of *spiniger* and *zimmermanni*, in several cases mixed up with other *Lepthyphantes* species as well.

The species was collected in the entrances of caves and in dolines, but also outside caves in the litter stratum of coniferous forests.

***Lepthyphantes floriana* Van Helsdingen, spec. nov.**  
(Fig. 31-34, 63)

*Lepthyphantes zimmermanni*; Niculescu-Burlacu, 1968: 91 (Rumania).

Types. — Holotype ♂ from Branesti, near Bucarest, Rumania (ML); many ♀ and ♂ paratypes from the same locality (ML and Institutul de Biologie "Traian Savulescu" at Bucarest).

Specimens of this species were doubtfully referred to *L. zimmermanni* by one of us (vH) when he advised Miss Burlacu in 1967 during her faunistic research in the Branesti wood near Bucarest. In the course of our present review we realized that a set of constant differential characters neatly separates this population from *zimmermanni* and the other species of this group, and that we are dealing with a separate species of the *zimmermanni* subgroup. It is a pleasure to name this species after Mrs. Floriana Niculescu-Burlacu.

Diagnosis. — A species of the *tenuis* group, which closely resembles *zimmermanni* but differs in the dentition of the paracymbium, having two teeth instead of one; the shape of the lamella is also different. The lateral wings of the inner scape in the epigyne are of more angular shape than in *zimmermanni* and *spiniger*. The stridulating files (Fig. 63) are finer, with the ridges closer together than in *zimmermanni*, but not as fine as in *spiniger*. The legs, especially the femora, are conspicuously whitish yellow.

Measurements (mm). Total length, ♀ 2.5-2.7, ♂ 2.0-2.6; length cephalothorax, ♀ ♂ 1.0-1.1. Legs: Fe I 1.15-1.3 times length cephalothorax in females, 1.2-1.3 times in males.

Male palp (Fig. 31-33) with the paracymbium furnished with two teeth at the posterior margin, the upper one pointing downward, the lower one slightly larger and pointing upward, thus enclosing a roundish dent between them. Lamella with a dorsal lobe above the main lateral branch, dorsal and ventral branches after the curve rather short. Base of embolus with few denticles or none, this character being variable. Length of cymbium 0.40-0.44 mm.

Epigyne (Fig. 34) hardly differing from that of *zimmermanni*, but the wing-like extensions of the inner scape with a distinct posterior angle and often with an additional projection just in front of broadest point, giving the wings an angular appearance. Posterior median plate largely covered by the wings of the inner scape and thus less conspicuous than in *zimmermanni*. Width of basal part of scape 0.175-0.190, of inner scape (measured between tips of wings) 0.185-0.200, of posterior median plate 0.210-0.240 mm.

Distribution. — *L. floriana* is described after specimens from Branesti forest near Bucarest, Rumania, where it appears to be very common. The specimens

were collected with Barber traps and inhabit the leaf litter stratum of deciduous forest.

A single ♀ specimen from Drensky's collection (Zoological Institute, Sofia) seems to belong to this species; it originates from Tscherepischki monastir near Iskar, Bulgaria, vi.1916, leg. P. Drensky, which suggests a wider distribution in the Balkans.

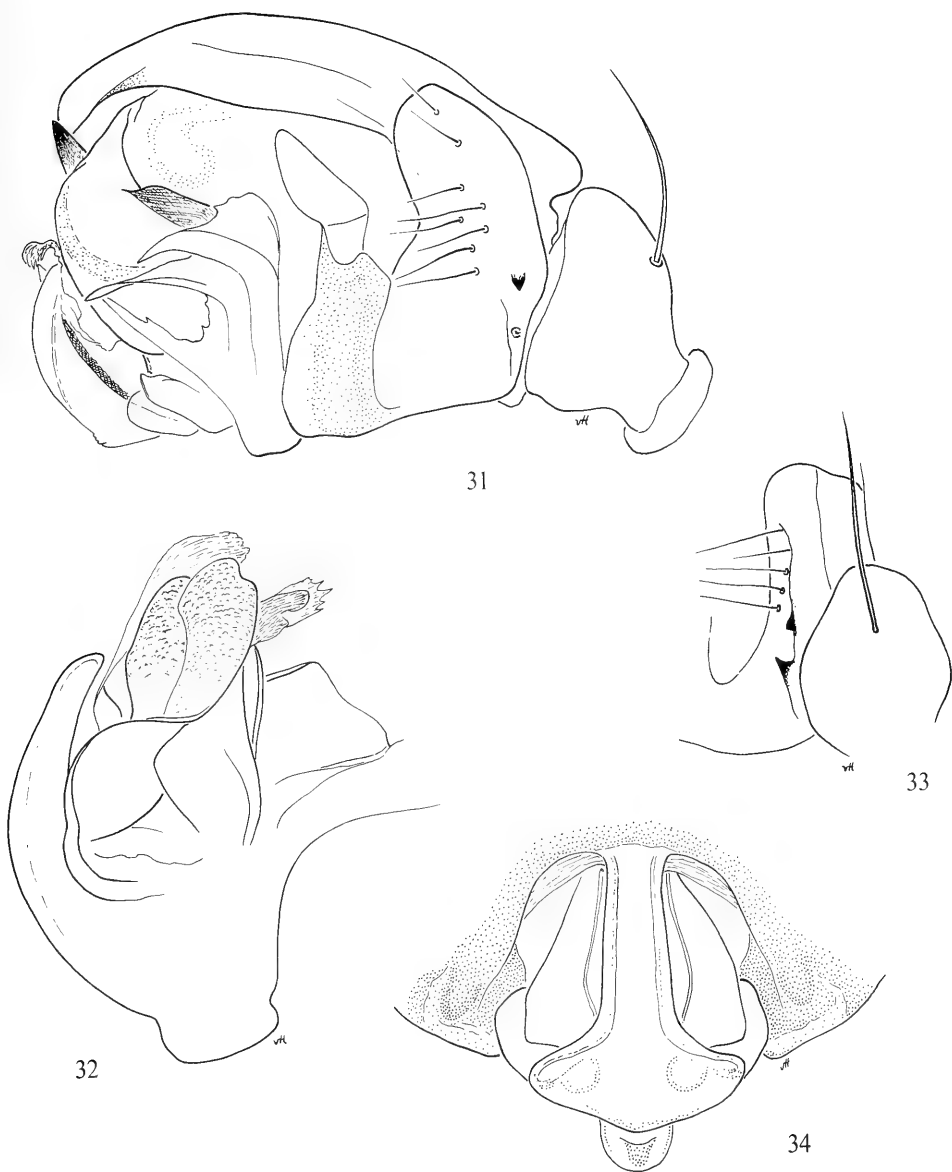


Fig. 31—34. *Lepthyphantes floriana* Van Helsdingen, spec. nov. 31, male palp, lateral aspect; 32, radical section, ventral aspect; 33, paracymbium; 34, epigyne. 33, X 142; 34, X 150; 31, 32, X 160

***Lepthyphantes tenebricola* (Wider)**  
(Fig. 35-38, 64)

*Linyphia tenebricola* Wider, 1834: 267, Pl. 18 Fig. 2 (descr. ♀; Germany).

*Lepthyphantes tenebricola*; Miller, 1947: 40, Pl. 13 Fig. 3 (♀). Locket & Millidge, 1953: 388, Fig. 230 D, 232 G (♀ ♂). Wiehle, 1956: 145, Fig. 327-330 (♀ ♂). Wanless, 1971: 23, 26, Pl. 3, Pl. 6 Fig. C (♀); 1973: 129, 134, Pl. 1 Fig. 2, Pl. 6 Fig. 2 (♀).

*Linyphia arcuata* Thorell, 1856: 168 (descr. ♀ ♂; Sweden).

*Lepthyphantes arcuatus*; Braun, 1960: 65 (used as oldest available synonym because the type-material of *Linyphia tenebricola* Wider was found to belong to another species; see, however, under remarks below); 1969: 215 (idem). Braun & Rabeler, 1969: 41 (idem).

**Remarks.** — Braun (1960), having been informed that the type-series of *Linyphia tenebricola* Wider (in SMF) did not belong to the species currently recognized under that name (in the combination *Lepthyphantes tenebricola*), but to *Lepthyphantes flavipes* (Blackwall), solved the problem by replacing *flavipes* Blackwall (from 1854) by the older *tenebricola* Wider (from 1834). *Lepthyphantes tenebricola* auct. consequently had to be replaced by the oldest available synonym, *Linyphia*

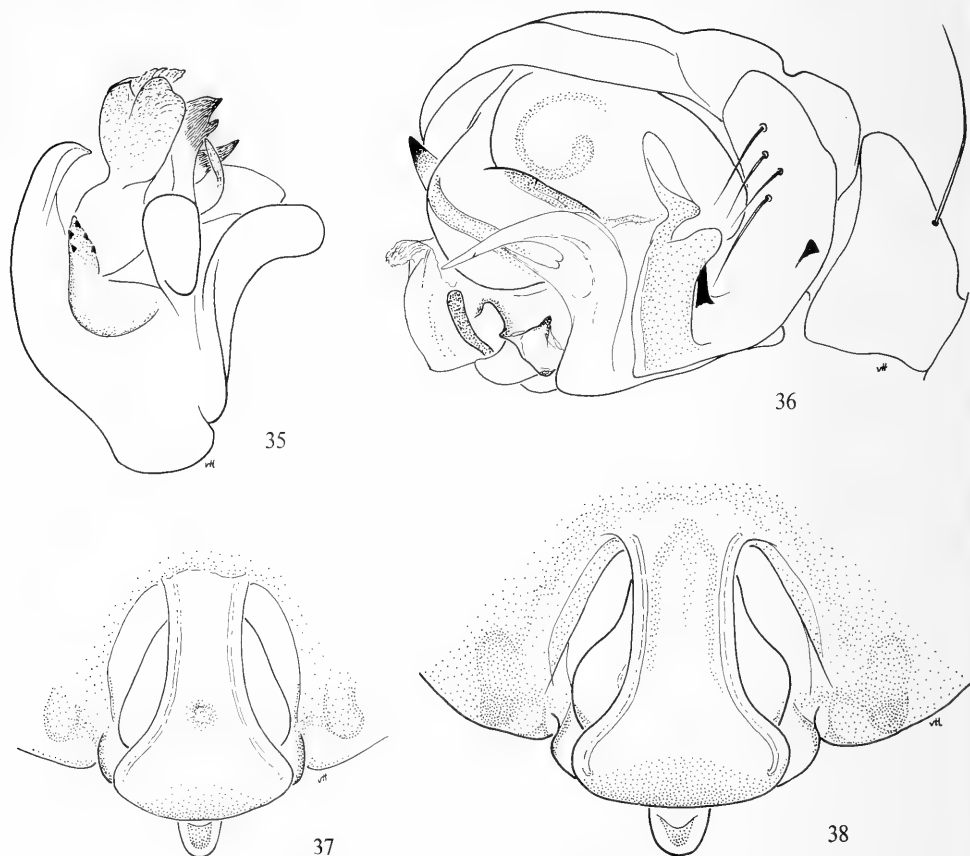


Fig. 35—38. *Lepthyphantes tenebricola* (Wider). 35, radical section, ventral aspect; 36, male palp, lateral aspect; 37, epigyne (specimen from French Jura); 38, epigyne (specimen from Holland). 37, X 135; 35, 36, X 144; 38, X 158

*arcuata* Thorell, 1856. Subsequently it was found that the one misidentification had been replaced by another (Locket, Millidge & Van Helsdingen, 1970: 90), as the type-specimens were found to belong to *Lepthyphantes menzei* Kulczyński, 1887, and not to *L. flavipes* (Blackwall). Straightforward nomenclatorial procedures would ask for another shifting of names, replacing *menzei* Kulczyński (from 1887) by *tenebricola* Wider (from 1834), using *arcuatus* Thorell (from 1856) for *tenebricola* auct., and re-establishing *flavipes* Blackwall in its original sense. However, it is thought highly inadvisable to carry through such a shifting of names for so common and frequently used names — not only by taxonomists. A proposal to stabilize the situation has therefore been presented to the International Commission on Zoological Nomenclature (see Locket, Millidge & Van Helsdingen, 1970). We deal with the species in the current sense here.

The synonymy of *Linyphia arcuata* Thorell with the species currently referred to as *Lepthyphantes tenebricola* (Wider) is difficult to ascertain, unambiguous type-material of *arcuata* not being available.

**Diagnosis.** — The species is easily recognized by the dentition of the paracymbium and the relatively simple lamella. The epigyne has a comparatively broad basal portion of the visible scape.

**Measurements** (in mm). Total length, ♀ 2.2-2.8, ♂ 2.15-2.35; length cephalothorax, ♀ 0.92-1.12, ♂ 0.97-1.05. Legs: Fe I 1.1-1.2 times cephalothorax in females, 1.1-1.25 times in males.

Stridulating files (Fig. 64) coarse at base, finer at apex.

**Male palp** (Fig. 35, 36): paracymbium with two teeth on the basal branch, viz., a blunt one near the posterior margin and a long and slender one behind the distal branch when seen from the side, but revealed in full length when viewed slightly from behind. Lamella sickle-shaped, its outer (dorsal) curve with or without an additional branch, of comparatively simple shape. Base of embolus with 3 to 7 denticles. Length of cymbium 0.36-0.39 mm.

The variation observed in the palp of *tenebricola* concerns the size of the large, distal tooth on the paracymbium, the shape of the lamella, and the number of denticles on the base of the embolus. As to the lamella, it has already been pointed out above that the outer margin may have a separate short branch dorsally, otherwise this branch is only indicated by a small denticle. The number of denticles on the basal section of the embolus varies from three to seven.

**Epigyne** (Fig. 38) with basal part of scape gradually widening from the relatively broad anterior section (two-fifths to one-half of maximum width of scape) to the broadly rounded posterior margin where the scape turns dorsad and inward; at this point the scape is conspicuously dark brown, a sign of heavy sclerotization, distinguishing it at once from most other species recognized so far; lateral wings of inner scape with tips as far apart as width of basal part of scape or slightly less, and rounded, never angular. Posterior median plate visible at either side of scape, but not very conspicuously so. Width of basal part of scape 0.175-0.215, of inner scape 0.150-0.190, of posterior median plate 0.200-0.240 mm.

The epigyne quite obviously is subject to a relatively large variation. Not only the ratio width anterior section to width posterior section of the basal part of

the scape varies between 0.4 and 0.5 (which makes quite a different impression), but there also is a large amount of variation in the development of a median pit or depression at half length of the basal part of the scape. This pit can be quite conspicuous because of the stronger pigmentation (sclerotization) of the surrounding area (rare), or it merely consists of a slight depression with only the slightest pigmentation. We have seen well pitted scapes in specimens from the French Jura (Fig. 37) and from Graubünden in Switzerland. The lateral wings of the inner scape are rounded with a straight or slightly concave margin in front of the broadest point.

Distribution. — Bonnet could list references for nearly the whole of Europe, with the exception of Iceland and Greece. Moreover, the species had been found on the Açores, Madeira, and in Kamtchatka.

Since 1940, the species has again been recorded from many countries in Europe. The only record from Madeira (Simon, 1897), based on a single adult female (MP, examined), was already disputed by Denis (1962: 77, 108) and is here referred to *tenuis*. We have not seen the specimens from the Açores. The material from Kamtchatka certainly needs to be re-examined.

The species is said to occur also in caves (records from Switzerland and Hungary, see Wolf, 1934-1937). It is certainly not a troglophilous species and may have been found near the entrances only.

Our observations are based on material from Austria (common), Czechoslovakia (common), Switzerland (common), Italy, Bulgaria and Holland (infrequent). Figures based on specimens from Holland. It is a widespread species and usually referred to as not uncommon in the leaf-litter stratum in forests. It is common in the Swiss and Austrian Alps (up to 2,000 m). Most adult specimens were collected in the summer (Braun & Rabeler, 1969: 41, sub *arcuatus*; Palmgren, 1975: 59).

### ***Lepthyphantes jacksoni* Schenkel**

(Fig. 39-42, 65)

*Lepthyphantes jacksoni* Schenkel, 1925: 266, 302, Fig. 10 A-D (descr. ♀ ♂; Wallis, Switzerland); 1927: 229 (Wallis); 1929: 10 (Tessin); 1933: 15 (Wallis). Forcart, 1961: 72 (designation of lectotype).

*Lepthyphantes tenebricola*; Schenkel, 1929: 10 (p.p.; Tessin).

Types. — The original material of this species is preserved in the Basel collection, together with that of later records. A male, bearing the label "Weg vom Hotel zum Märjelensee" was selected lectotype by Forcart (1961). A female from "Weg vom Hotel Jungfrau zum Eggishorn" is the only paralectotype.

Diagnosis. — *L. jacksoni* belongs to the species-subgroup with a pit or depression in the scape of the epigyne and a single large tooth on the paracymbium. It can be distinguished from the other member of the subgroup in the Alps by the shape of the lamella which has the two branches clearly diverging; in *jacksonoides* the branches run parallel.

Measurements (in mm). Total length, ♀ 2.2-2.5, ♂ 1.95-2.2; length cephalothorax, ♀ 0.96-1.08, ♂ 0.90-1.08. Legs: Fe I 1.15-1.25 times length cephalothorax in females, 1.1-1.2 times in males.



Stridulating files rather coarse (Fig. 65).

Male palp (Fig. 39-41). Paracymbium with a single, fair-sized tooth close to the inner margin of the distal branch and thus not visible in the lateral aspect, but quite conspicuous in postero-lateral view. Lamella forked, both branches well-developed, diverging (cf. *jacksonoides*), dorsal branch pointing forward, ventral branch longest and curved antero-ventrally. Terminal apophysis with a well-developed and sclerotized ventral lobe, which is blade-like and curved upward. Base of embolus with 1-4 denticles. Length of cymbium 0.42-0.45 mm.

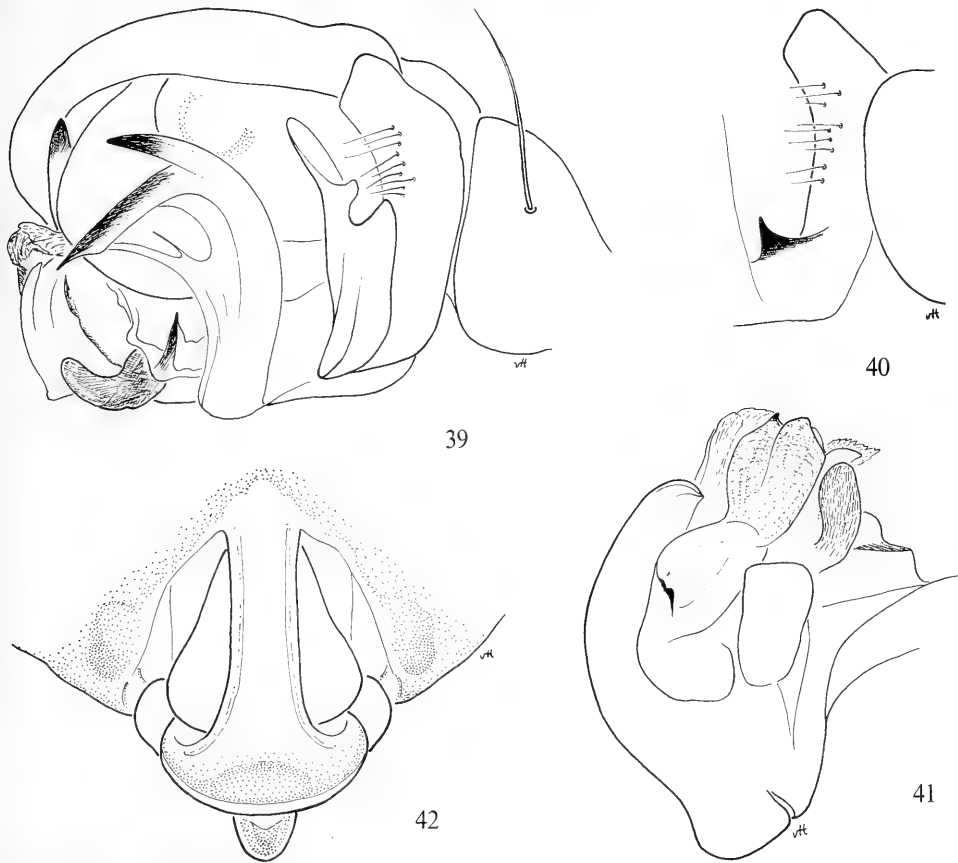


Fig. 39-42. *Lepthyphantes jacksoni* Schenkel. 39, male palp, lateral aspect; 40, paracymbium; 41, radical section, ventral aspect; 42, epigyne. X 142

Epigyne (Fig. 42). Basal part of scape with parallel-sided stem, widening into the much broader posterior section which bears a characteristic, oval depression just in front of the transition of basal part into inner scape; lateral wings of inner scape rounded or slightly angular, inner scape at this point nearly as wide as broadest, posterior section of basal part. Posterior median plate distinctly wider than scape. Width of basal part of scape 0.200-0.215, of inner scape 0.185-0.190, of posterior median plate 0.250 mm. In the lateral aspect the strong curvature of the basal part of the scape and the depression near the tip are distinct.

Distribution. — Up to the present the species had only been recorded by Schenkel from Wallis and Tessin in Switzerland. All Schenkel's specimens (see below) were collected in July and August, and above 2,000 m, but the number of records is too scanty yet to consider these data as the absolute limits in time and distribution. It is not unlikely that, as in *jacksonoides*, the species lives outside forests in the herbal stratum, up to 50 cm above the soil, rather than close to the ground in leaf-litter, moss, and between the lower parts of grasses and herbs.

In the eastern Alps, *L. jacksoni* seems to be replaced by another species of this subgroup, *L. jacksonoides*. The latter has been found at 1,500 m and above in northern and eastern Switzerland, the Austrian Alps, and in Bulgaria. We do not know if and where the distributions of the two species meet or overlap. In fact, this kind of information might serve to evaluate the characters here used to distinguish between the two species.

All specimens mentioned by Schenkel in subsequent years have been re-examined. The only additional material that can be recorded here consists of 3 ♀ from Bedretto (Tessin), vii-viii, which were found in the collection of the Naturhistorisches Museum at Basel among specimens of *L. tenebricola* (Wider) and published under that name by Schenkel (1929: 10, p.p.).

The available material is listed here for completeness sake (all preserved in NMB).

Wallis: 1 ♂, Bez. Goms, Weg vom Hotel Jungfrau zum Märjelensee, 2190-2390 m, 21.vii.1923, E. Schenkel (lectotype); 1 ♀, Weg vom Hotel Jungfrau zum Eggishorn, oberer Teil, 2400-2934 m, 7. vii.1924, E. Schenkel (paralectotype). 1 ♀ 1 ♂, Umgebung Saas Fee, vii-viii; 2 ♀ 1 ♂, linker und rechter Talhang bei [Saas] Almagel, vii., figured.

Tessin: 1 ♂, Bedretto, rechter Talhang, vii; 3 ♀, Bedretto, vii-viii (*L. tenebricola*, Schenkel, 1929, p.p.).

### ***Lepthyphantes jacksonoides* Van Helsdingen, spec. nov.**

(Fig. 43-46, 66)

*Lepthyphantes nigriventris*; Schmölzer, 1962: 269 (Austria, Nordtirol).

*Lepthyphantes* spec. nahe *jacksoni*; Palmgren, 1973: 31, Fig. 2 (Austria: Nordtirol, Kärnten, Salzburg).

This new species closely resembles *L. jacksoni* Schenkel, from which it can be distinguished by the shape of the lamella in the male palp, the stridulating files, and (tentative conclusion) by its distribution.

Types. — ♂ holotype from Austria, Osttirol, Umbaltal W. of Prägraten, 1300-1550 m, 4.viii.1973, P. J. van Helsdingen, from herbage along river; 2 ♀ 2 ♂, paratypes, collected with the holotype (whole series in ML).

Description. — Measurements (in mm). Total length, ♀ 2.15-3.2, ♂ 2.2-2.9; length cephalothorax, ♀ 1.0-1.22, ♂ 1.0-1.25. Legs: Fe I 1.1-1.25 times length cephalothorax in females, 1.1-1.3 times in males.

Coloration. Cephalothorax grey-brown, blackish-grey along margins. Legs light brown. Abdomen with light dorsal and lateral surfaces, not unlike *tenuis*, at first

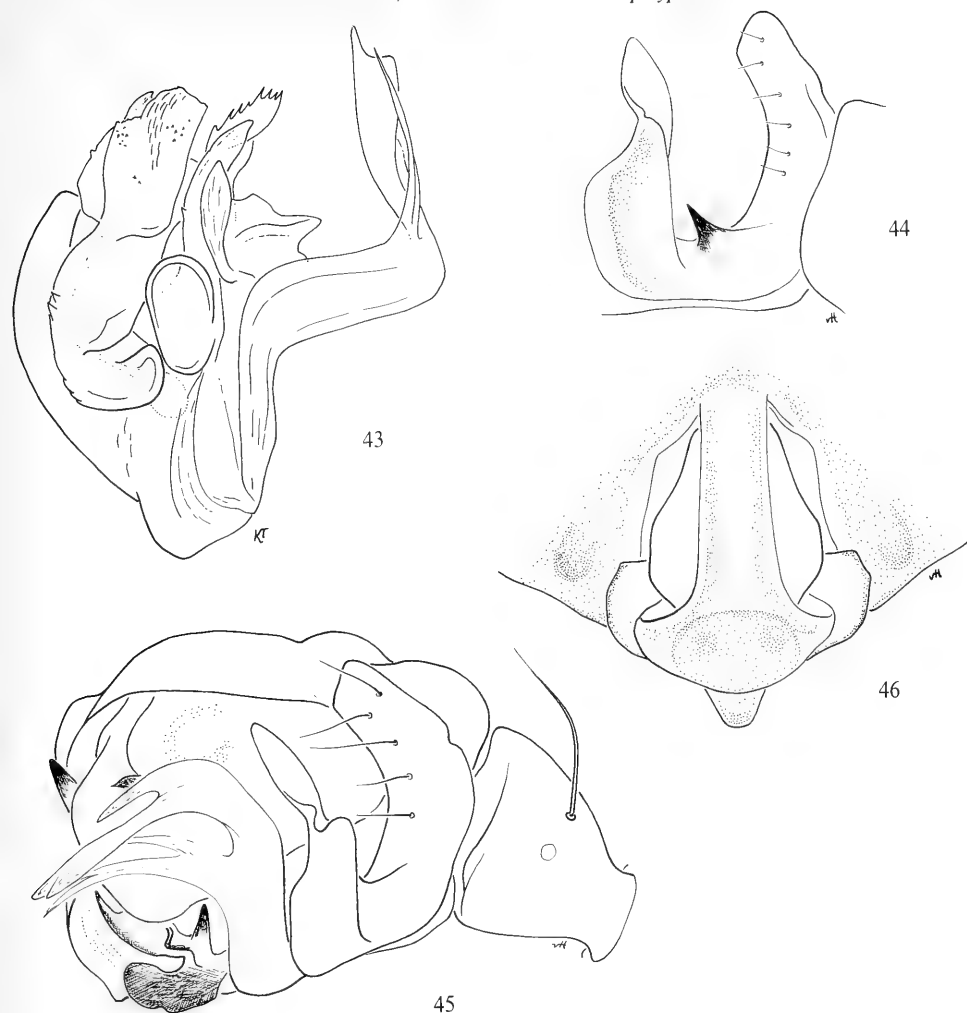


Fig. 43—46. *Lepthyphantes jacksonoides* Van Helsdingen, spec. nov., 43, radical section, ventral aspect; 44, paracymbium; 45, male palp, lateral aspect; 46, epigyne. 44—46, X 128; 43, X 265

sight; dark grey V-shaped markings narrow or interrupted in the middle and light lateral stripe broadly connected with the light areas of the dorsal surface, lighter areas strewn with many white blotches. In males pattern much reduced, but often still visible.

Stridulating files (Fig. 66) rather fine, especially basad, ridges closer together than in *jacksoni*.

Legs with the usual set of spines, as indicated for the genus. Position of retrodorsal (basal) spine on tibia I 0.29-0.34, length of this spine 0.31-0.35 mm in ♀, 0.21-0.28 mm in ♂. Tm I 0.20-0.26.

Male palp (Fig. 43-45). Resembling in general the palp of *jacksoni* but differing in the following respect. Dorsal and ventral branches of the lamellar tip not diverging (cf. Fig. 39), but dorsal branch slightly curved and roughly parallel to ventral one. Length of cymbium 0.40-0.47 mm (*jacksoni*: 0.42-0.45).

Epigyne (Fig. 46) hardly different from that of *jacksoni*, with the same kind of depression near the tip of the basal part of the scape. Width of basal part of scape 0.210-0.225, of inner scape 0.160-0.190, of posterior median plate 0.250-0.275 mm.

Distribution. — So far known to occur in Switzerland (Glarus, Graubünden) and Austria (Vorarlberg, Nordtirol, Osttirol, Salzburg, Kärnten). A female specimen from Bulgaria (in cave "Dupocheto" near Velingrad, distr. Pazardjik) is thought to belong to *jacksonoides*, indicating a much wider distribution, but confirmation at the specific level has to wait until males become available from that area. Collected above 1,300 m and up to 2,400 m. It appears that the webs are (always ?) built in the vegetation at some distance from the soil (up to 50 cm), which is quite unusual for species of the *tenuis* group. The webs are thus more easily detected than in most other species of the group. Collecting dates range from June to September.

Rich material was available from Austria, mainly Nordtirol (figured), but the description of the species is largely based on the following specimens.

Switzerland: 1 ♀ 2 ♂, Glarus, Stausee Garichti near Schwanden, 1500-1600 m, 9.ix.1972, P. J. van Helsdingen, in herbage (ML). 2 ♀ 1 ♂ (palp only), Grisons (= Graubünden), Dr. Carl (MHNG) (not included in the type-series).

Austria: 1 ♂, Nordtirol, Zillertaler Alpen, Höllensteinloch, 1949, H. Janetschek (NMB). 2 ♀ 3 ♂, Osttirol, Umbaltal W. of Prägraten, 1300-1550 m, 4.viii.1973, P. J. van Helsdingen, from herbage along river (type-series; ML).

### ***Lepthyphantes nigriventris* (L. Koch)**

(Fig. 47-49. 67)

*Linyphia nigriventris* L. Koch, 1879: 34, Pl. 1 Fig. 22-22a (descr. ♀, Siberia, Yenisey region).

*Lepthyphantes nigriventris*; Kulczyński, 1916: 20, Pl. 1 Fig. 29 (*nigriventer*; ♀, Siberia). Ermolajev, 1934: 138 (West Siberia). Holm, 1945: 8 (Sweden), 54, Fig. 16 a-d (descr. ♂, genitalia depicted); 1951: 144 (Swedish Lapland); 1952: 122 (Swedish Lapland); 1973: 71, 95, Fig. 73-74 (redescription of type-material, lectotype selected). Brinck & Wingstrand, 1949: 27. Hackman, 1954: 5, 53 (Newfoundland).

Types. — The original material of Koch consisted of 3 ♀ from the Yenisey region, Siberia. A lectotype (from Krasnoyarsk) was selected by Holm (1973: 95). All specimens are preserved in the Naturhistoriska Riksmuseet at Stockholm. We have examined the lectotype and one paralectotype.

Schmölzer's record (1962: 269) probably belongs to the closely related species from the eastern Alps, *L. jacksonoides* spec. nov.

Diagnosis. — *L. nigriventris* belongs to the *jacksoni* subgroup, which is characterized by the pit or depression in the scapus of the epigyne, and by the laterally projecting lamellate structure of the terminal apophysis in the male palp. In *nigriventris* this projection is relatively short, and the position of the tooth on the paracymbium is also different from the other species of the subgroup.

Measurements (in mm). Total length, ♀ 2.9-3.4, ♂ (one specimen only) 2.6;

length cephalothorax, ♀ 1.23-1.32, ♂ 1.22. Legs: Fe I 1.2-1.3 times length cephalothorax in females, 1.33 times in male.

Stridulating files (Fig. 67) fine, ridges close together.

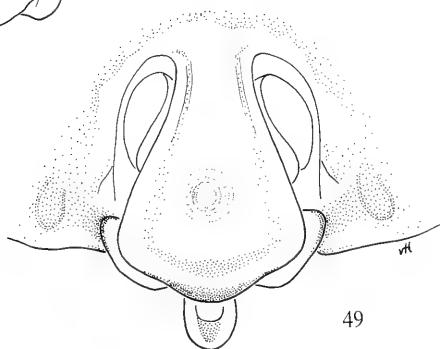
Male palp (Fig. 47, 48). Paracymbium with a single, large and slender tooth on



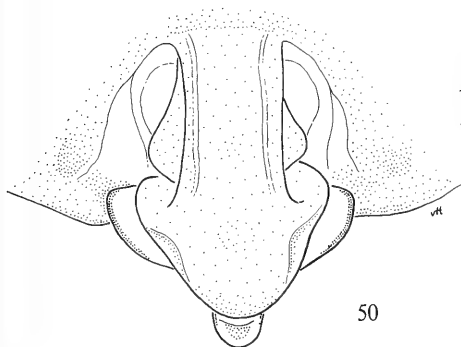
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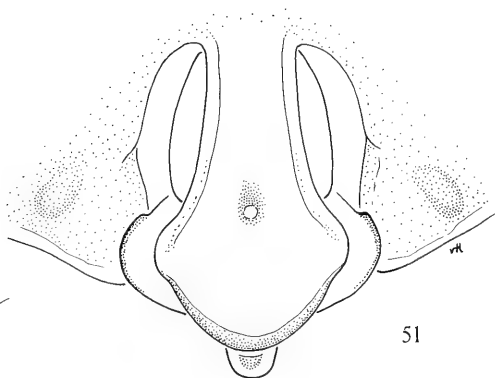
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Fig. 47—49. *Lepthyphantes nigriventris* (L. Koch). 47, male palp, lateral aspect; 48, radical section, ventral aspect; 49, epigyne. Fig. 50—51. *L. camtschaticus* Kulczyński. 50, epigyne (holotype); 51, epigyne (specimen mentioned by Schenkel, 1930). X 128

the proximal branch, close to the posterior margin, and not at the base of, and hidden behind, the distal branch (cf. *jacksoni* and *jacksonoides*). Lamella with diverging dorsal and ventral branches, both rather straight. Terminal apophysis with a lateral blade-like projection which is rather short and rounded (cf. *jacksoni* and *jacksonoides*). Embolus without denticles on the basal ridge (cf. *jacksoni* and *jacksonoides*). Length of cymbium (of specimen from Torne Träsk) 0.46 mm.

Epigyne (Fig. 49) with a distinctly pitted scape; basal part of scape gradually widening posterad; lateral lobes of inner scape rounded, inner scape about as wide as the basal part; posterior margin of basal part sclerotized, reminding of *tenebricola*. Posterior median plate distinct in the ventral aspect of the epigyne. Width of basal part of scape 0.180-0.200, of inner scape 0.165-0.200, of posterior median plate 0.235-0.250 mm.

Distribution. — Bonnet summarizes the distribution of this species as Norway, Sweden, Siberia. It has been found on several occasions in Swedish Lapland (Holm, 1945, 1951, 1952; Brinck & Wingstrand, 1949), while the original material of *L. Koch* from Siberia (Yenissey valley) was redescribed by Holm (1973: 95). A single female has been recorded from Newfoundland (Hackman, 1954). We have re-examined the specimen (Zoological Museum, Helsinki) and agree with the identification; the lighter areas of the abdomen are strewn with white blotches, a feature we have not observed in other specimens. *L. camtschaticus* Kulczyński, from Kamtchatka, might belong to this species, though the shape of the epigyne (no males known) is slightly different from that of *nigriventris* (see also the general discussion, p. 46).

According to Dr. T. Kronestedt of Stockholm (pers. comm.) the webs of this species are, again, found in the vegetation at some distance above the ground level (see also under *jacksonoides*), not close to the surface as in most other species of the *tenuis* group.

Material examined. — We have seen the lectotype and one paralectotype from the Yenissey region (Briochowskij Islands, Chantajskoj, Krasnojarsk) (NRS). From Swedish Lapland we received specimens from Mr. T. Kronestedt: 1♂ 2♀, Torne Lapmark, N. of Torne Träsk Lake, south side of Lullehatjärro mountain, 20-27.viii.1969, T. Kronestedt (ML).

Canada: 1♀, Newfoundland, St. Barbe Isl., Docters Hill, 29.vi.1949, E. Palmén, from litter (Zoological Museum, Helsinki).

The figures are based on the specimens from Swedish Lapland.

### ***Lepthyphantes camtschaticus* Kulczyński**

(Fig. 50, 51)

*Lepthyphantes camtschaticus* Kulczyński, 1926: 33, 57, Pl. 2 Fig. 19 (descr. ♀; Kamtchatka). Schenkel, 1930: 17, Fig. 6 (descr. ♀; Kamtchatka). Holm, 1973: 95, Fig. 75 (compared with *L. nigriventris*).

Type. — The ♀ holotype is preserved in the collection of the Zoological Institute at Warszawa (examined); it originates from Klutschevskoje, Kamtchatka.

**Diagnosis.** — *Lepthyphantes camtschaticus* belongs to the *jacksoni* subgroup according to the median pit in the scape of the epigyne (absent in the holotype!). Only two specimens have ever been mentioned in the literature, both females. From these specimens it appears that the shape of the scape is slightly more prolonged than in *L. nigriventris*. It is difficult, at this moment, to assess the value of this character, because eastern Siberia is so poorly collected and no male specimens have become available as yet. It is not impossible that we are dealing with one polytypic species, which occurs in northern Europe (*nigriventris*), Siberia (*nigriventris*), Kamtchatka (*camtschaticus*), and the Nearctic region (Newfoundland; *nigriventris*) (see also the general discussion, p. 46).

Measurements (in mm). Female. Total length 3.4, length cephalothorax 1.20-1.37, Fe I 1.3 times as long as cephalothorax.

Stridulating files fine.

Epigyne (Fig. 50, 51). The distal end of the basal part of the scape is more prolonged posterad, thus giving it a more slender appearance; however, the width is the same as in *nigriventris* (0.20 mm). In the holotype, no pit is visible on the basal part of the scape, but in the specimen from Achomtenbay (Schenkel, 1930) a well-developed pit is present (Fig. 51).

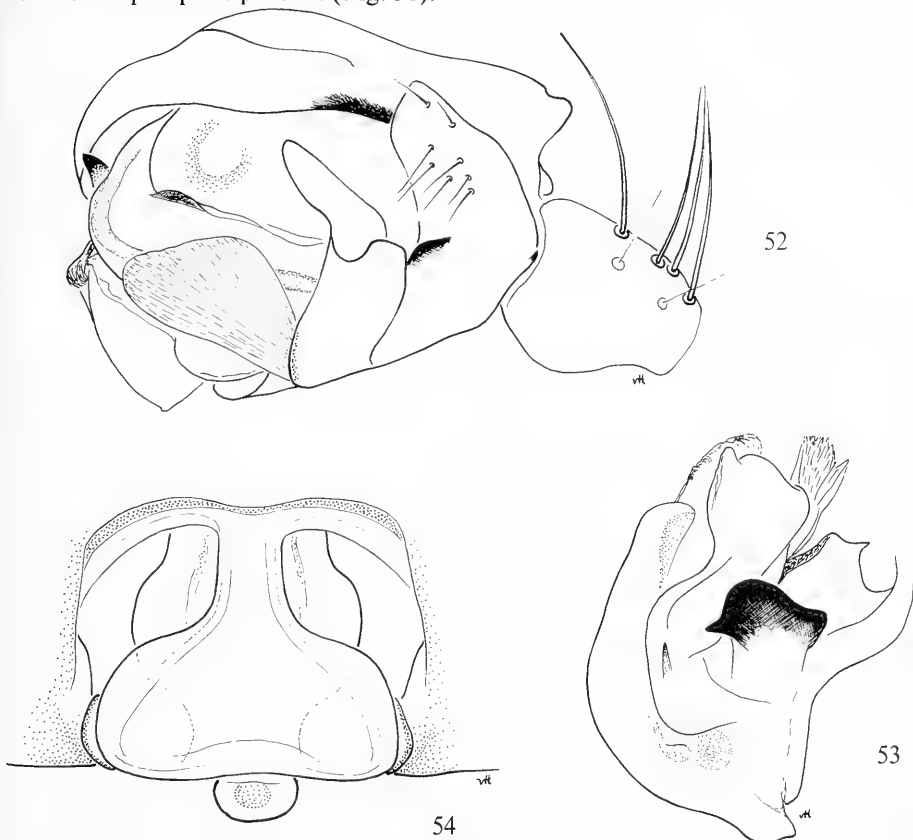


Fig. 52—54. *Lepthyphantes cristatus* (Menge). 52, male palp, lateral aspect; 53, radical section, ventral aspect; 54, epigyne. 52, 53, X 150; 54, X 220

Distribution. — Kamtchatka.

Material examined. — We have studied the ♀ holotype from Kamtchatka, Klutschevskoje, 10.viii.1909 (Warszawa), and the single ♀ specimen recorded by Schenkel (1930) from Achomtenbay, Kamtchatka (NRS).

### ***Lepthyphantes cristatus* (Menge)**

(Fig. 52-54, 68)

*Bathyphantes cristatus* Menge, 1866: 121, Pl. 22 Fig. 46 (descr. ♀ ♂; Poland (Danzig)).

*Lepthyphantes cristatus*; Miller & Kratochvil, 1948: 139, 140, Fig. 2 a-d (compared with *L. pallidiventrīs*).

Locket & Millidge, 1953: 386, Fig. 230A, 232E (♀ ♂). Wiehle, 1956: 192, Fig. 319-326 (♀ ♂). Wanless, 1971: 22, 26, Pl. 2, Pl. 6 Fig. E (♀); 1973: 129, 134, Pl. 1 Fig. 3, Pl. 6 Fig. 3 (♀).

*Lepthyphantes cristatus pallidus* Miller & Kratochvil, 1938: 238, 242, Fig. 3 (descr. ♀; Czechoslovakia).

*Lepthyphantes pallidiventrīs* Miller & Kratochvil, 1948: 139, 140, Fig. 2 e-h (nom. nov. pro *L. pallidus* Miller & Kratochvil, brought to species level; compared with *L. cristatus*; ♀ and ♂).

Remarks. — Miller & Kratochvil (1938) described a subspecies of *cristatus* from Czechoslovakia, which they subsequently raised to species level and, obligatory, renamed *pallidiventrīs* (1948). We have examined material kindly sent to us by Dr. Miller, and we did not find any substantial differential characters, notwithstanding the apparent differences which can be observed in the 1948 illustrations (Fig. 2, a-d, *cristatus*, e-h, *pallidiventrīs*). We are, therefore, of the opinion that *pallidiventrīs* is nothing but an extremely light-coloured form of *cristatus*. Specimens of this kind are frequently found, together with normally coloured specimens of *cristatus*, in Nordtirol, and a subspecific status is therefore out of the question. Consequently *L. pallidiventrīs* is listed in this paper as a junior synonym of *cristatus*.

Diagnosis. — *L. cristatus* takes an isolated position in the *tenuis* group because of the horned cymbium, the occurrence of several tibial spines in the male palp, and the deviating chaetotaxy.

Measurements (in mm). Total length, ♀ 2.3-2.7, ♂ 2.2-2.4; length cephalothorax, ♀ 0.95-1.05, ♂ 1.02-1.25. Legs: Fe I 1.1-1.25 times length cephalothorax in ♀, 1.2-1.3 times in ♂.

Stridulating files fine (Fig. 68). Posterior tibiae (III and IV) with a retrolateral spine and thus differing from the other species of the *tenuis* group.

Male palp (Fig. 52, 53) at once distinguished from the other species of the group by the presence of four spines on the tibia and small tubercles at the proximo-lateral and proximo-mesal corners of the cymbium. Paracymbium with posterior margin slightly convex posterad and bearing a narrow ridge there which ends in a small sharp tooth at its dorsal limit; a serrate crest-like elevation at the base of the distal branch. Radix as usual, with the exception of the Fickert's gland, which appears to be modified in this species: the gland is followed distally by a second inflated, but less spherical, section of the spermduct. Distal section of lamella a simple flat structure, which fans out from the narrow base. Basal section of terminal apophysis strongly sclerotized and protruding. Basal section of embolus with one or two slender, tooth-like protrusions. Length of cymbium 0.44-0.51 mm.

Epigyne (Fig. 54) with basal part of scape rather suddenly widening from narrow "stem" to comparatively broad posterior section with rounded tips; lateral wings



of inner scape roundish and gradually excavated anterad. Posterior median plate well visible but not much wider than basal part of scape. Width of basal part of scape 0.175-0.200, of inner scape 0.135-0.150, of posterior median plate 0.200-0.215 mm.

Distribution. — Up to 1940, *L. cristatus* had been recorded from nearly all European countries, with the exception of Greece, Portugal and Spain. European U.S.S.R. formed the eastern boundary, the Balkans and northern Italy were the southern limits. In the north-west there were records from Iceland and Greenland, but Braendegård (1958: 86) correctly pointed out that Jackson's (1930: 654) record of *cristatus* is to be found in an appendix on the Icelandic spider fauna at the end of his paper on the spiders of Greenland. Greenland thus has to be removed from the list of countries where the species has been found. Moreover, it appears now that in the Icelandic list Jackson only cites the older record for Iceland by Simon (1892: clxxvii) as do the other references to the occurrence on Iceland of *cristatus*. In the Paris collection a single male specimen from Iceland could be located which quite likely constitutes the material on which Simon's record was based. This specimen is not a *cristatus* but a *zimmermanni* and we therefore are inclined to believe that *L. cristatus* has never been found in Iceland.

A survey of the literature after 1940 revealed records of many of the European countries within the range indicated above, and also from northern Spain (Denis, 1962 b; Gerona).

The only cave records are by Drensky (1935: 98, 99, 102), from Yugoslavian caves.

We have examined material from Holland (not common), France, Austria (common), Czechoslovakia (common), and Yugoslavia. It is a species of the leaf litter and herbaceous layers in deciduous forests; in the Alps up to 1700 m, but in Scandinavia it is said to occur frequently in moors (Braun & Rabeler, 1969: 42; Palmgren, 1975: 59).

The figures are based on specimens from France (Dép. de l'Eure).

#### SPECIES INQUIRENDAE

The following species are considered to belong to the *tenuis* group, though their exact identity could not be established. It appeared either impossible to locate the type-material, or the specimens were incomplete and, therefore, unidentifiable.

*Lepthyphantes foliatus* Denis, 1945: 52, Fig. 1, Pl. 2 Fig. 25 (descr. ♀, Algeria).

The short description of the single female specimen Denis had before him when naming this species contains remarks on size and coloration. It is accompanied by a figure of the abdomen and a very small one of the epigyne. The latter is strongly suggestive of that of *L. tenuis* because of the anchor-shaped scape and the rounded lateral lobes. The size of the specimen agrees with that of *tenuis*, and so does the abdominal pattern, be it that in the latter the dark spots seem to be very contrasting with the lighter surroundings. *L. tenuis* is known to occur in Algeria,

and it is quite possible that Denis had this species in the small collection of spiders from that region he had received from the British Museum (Natural History), London. The only answer to this question would be a re-examination of the specimen, but neither Denis' private collection, now at the Muséum National d'Histoire Naturelle at Paris, nor the collection at London seem to contain the ♀ holotype of *L. foliatus*. Its loss during the war has been suggested.

*Lepthyphantes suldalensis* Strand, 1903: 10, 17, Fig. 2 a-b (descr. ♂, Norway).

The illustrations and description of this species strongly suggest it to belong to the *tenuis* group, even though Strand himself compared it with *Lepthyphantes obscurus* (Blackwall). The original specimens could be located in the Paris Museum. There are two specimens, a subadult ♂ and an adult ♂, but in the latter most legs and both palps are lacking. Thus we are deprived of the most reliable set of characters. The remnants of the adult specimen give us no decisive answer to the question of the identity. It is not very likely that there occurs a separate species in southern Norway and we tend to refer it to one of the other species of the *tenuis* group. Judging by the size of the adult specimen (length cephalothorax 0.90 mm, length Fe I 1.12 mm) it could be *mengei*, *flavipes*, or *tenuis* (excluding *herbicola* on zoogeographical grounds). However, the stridulating files and shape of the chelicerae exclude *flavipes* (which has a latero-basal boss and the stridulating files very coarse, if visible at all). Comparison with specimens of *mengei* and *tenuis* suggest the former, mainly because of the fine stridulating files. *L. mengei* is common in Scandinavia, while *L. tenuis* appears to be much rarer.

*Lepthyphantes tenoides* Kolosváry, 1938: 66, 74, Fig. b, c (descr. ♀, Yugoslavia).

All that can be said at present is that the epigyne reminds of that of *L. tenuis*, the very reason why it was called *tenoides*. It certainly belongs to the *tenuis* group, but without the specimen it is impossible to place the species more precisely.

#### Nearctic representatives of the *tenuis* group

Beside *L. tenuis* (Alaska, British Columbia, Washington) and *nigriventris* (Newfoundland) there are a number of species which occur in the Nearctic Region and probably belong to this species-group: *cracens* Zorsch, described from New York; *zebra* Emerton, occurring in the eastern United States; *zelatus* Zorsch, closely related to *zebra* and found in Washington; and *zibus* Zorsch, also from Washington. The reader is referred to the treatise on the genus *Lepthyphantes* in the United States by Zorsch (1937).

#### DISCUSSION

From the outset we intended to present a survey of the *tenuis* group of species: to provide useful means for the recognition of the species, to summarize the known distributions, and to erect a framework of reliable characters for establishing infra-group relationships and for a correct placing of species to be described in the future.

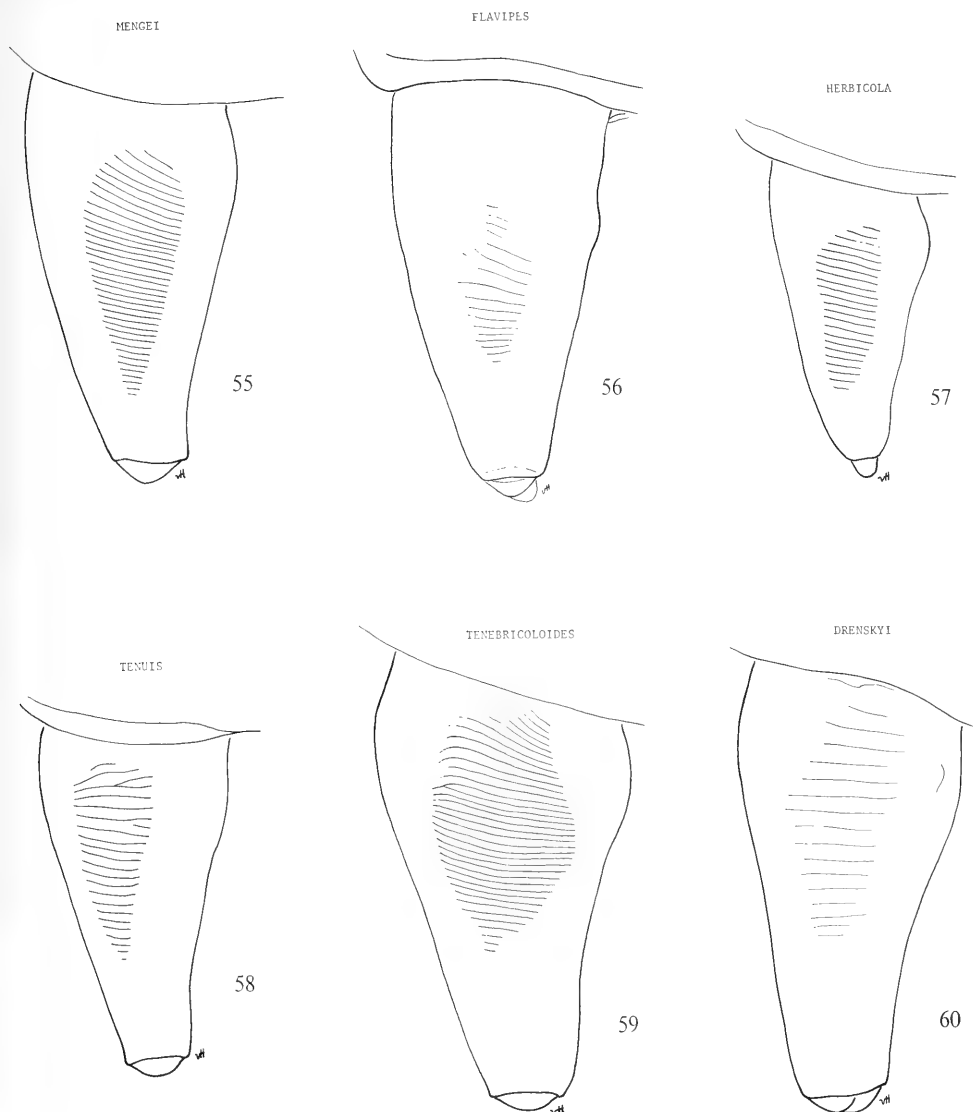


Fig. 55—60. Male chelicerae (but female of *flavipes*) of *Lepthyphantes* species, showing stridulating files. 59, X 112; 56, 58, 60, X 128; 57, X 135; 55, X 158

The approach had to be typological. The species treated here differ in a limited number of usable, mainly genital characters, and the differences are often so minute that variation is hard to trace. Apart from size and coloration, variation in the used differential genital characters only became apparent in a few instances, and then is discussed in the text. Most likely variability is as normal a phenomenon here as in other taxa, but it has to be studied independently, using more advanced methods such as scanning electron microscopy. In our present study it plays a minor role.

If one thing has become clear when studying this species-group, it is the poor state of knowledge of the group as a whole. This certainly is the result of inadequate literature, which, in the past, made it hard to identify a specimen at all. As pointed out in the introduction, we noticed a relatively high percentage of misidentifications in old collections. New species names appeared to have been proposed for specimens which in fact belong to the commonest members of the

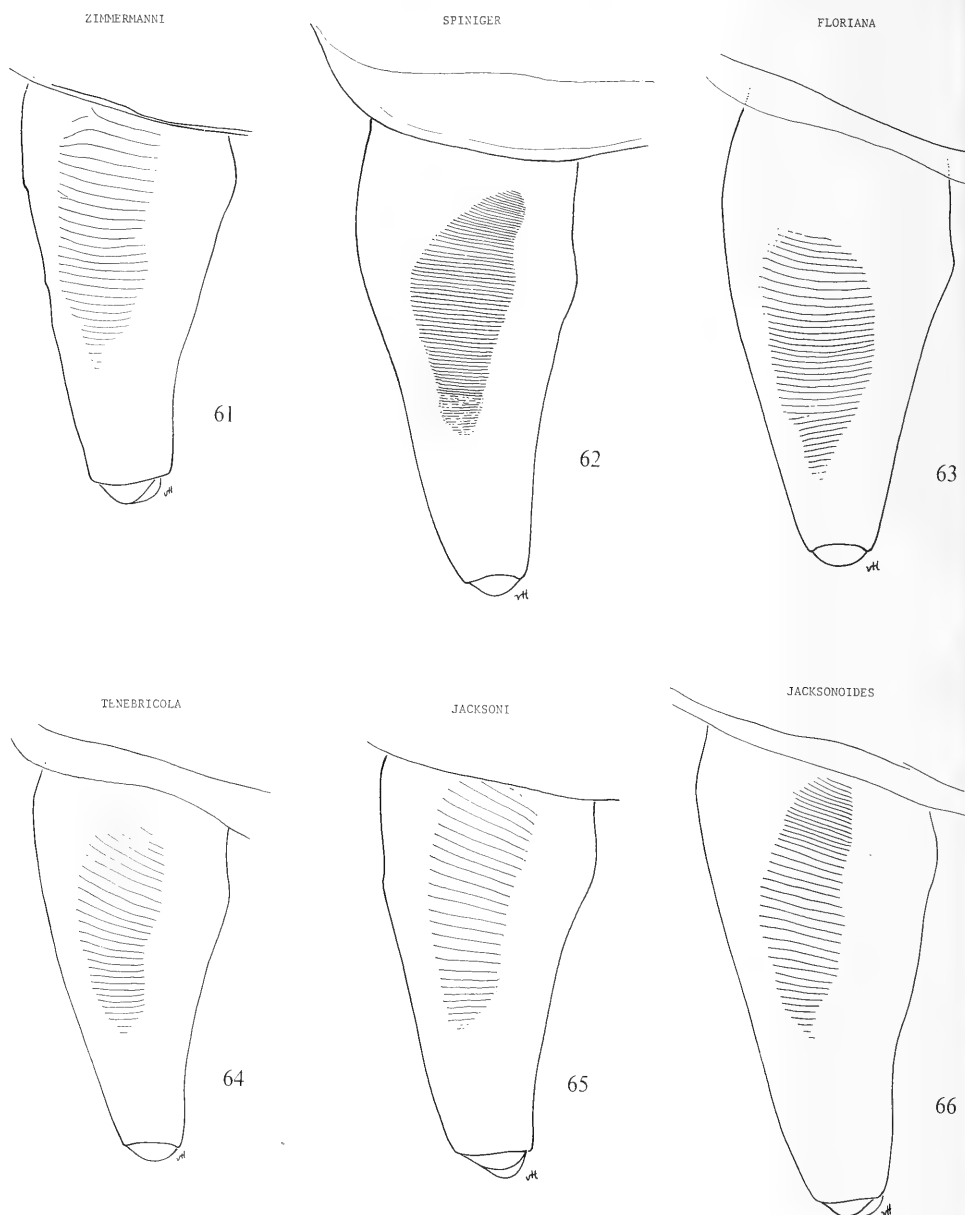


Fig. 61—66. Male chelicerae of *Leptyphantes* species, showing stridulating files. X 128

*tenuis* group. All this certainly did not help to clarify the dark points in our knowledge of the interspecific relationships, the diagnostic value of traditionally used characters, and the distributional patterns. Consequently we have attempted to improve upon the unsatisfactory situation. By doing so, we became much aware of all the existing gaps, many of which we are unable to fill at present. That our knowledge of the distribution of northern species such as *L. nigriventris* and *camtschaticus* is fragmentary is understandable because of the inaccessibility of these areas. But when we have to state that we really do not know anything certain about the distribution of *zimmermanni* in the Balkan Peninsula, we have to admit that this is the result of lack of interest rather than lack of opportunities. Even though the Swiss and Austrian Alps are easily accessible and indeed have been the field of activity of several arachnologists, we still lack insight in the distributions of several species (again *zimmermanni*, among others), including their altitudinal zonation. It was only recently that we discovered the existence of two alpine species in that area, *jacksoni* in the west and *jacksonoides* in the east, without being able to establish the boundary, or the zone of overlap, between the two as a result of insufficient collecting of "common" *Lepthyphantes* species.

#### Characters used.

Hardly paying any attention to coloration and abdominal patterns, which we suspect to be variable, we have incorporated size limits, proportional leg lengths, and chaetotaxy into the diagnosis. The chaetotaxy provide diagnostic characters in two cases only, viz., in *spiniger*, where the metatarsi bear more than the usual, single dorsal spine, and in *cristatus*, with its extra prolateral spines on tibiae III and IV.

The chelicerae show constant dentition through the whole group. The stridulating files, which are always present (with the *flavipes* ♂ as the only exception), have been used, more than before, to characterize species, though only in a comparative, qualitative way. The importance of this character lies in the assumption that it plays an active role in the maintenance of hybridization barriers, effectively isolating the species from each other. The organ is used during courtship, and we may assume that differently built stridulating files produce different vibrations in the web, and that positive response of a female is only evoked by a male of the same species, producing the right vibration. Comparative use of the files in the present paper is made possible by presenting figures of the male stridulating files of all species. A quantitative analysis has not been undertaken because several technical problems are involved, such as the changing interstices of the ridges of the files from base to apex. All epigynes are of comparable structure, i.e. a long sigmoid scape with a stretcher on top, arising from the anterior wall of an atrium, which at the posterior side is bordered by the medially incised posterior median plate. There is no reason to assume basic differences in the functional properties of the organ in the different species. Since the inner scape, apart from the shape of the lateral wings, has not been included in this study we cannot make use of these parts in differentiating the taxa. From Wanless' study (1973) of the epigynes of the British species of this genus it is clear that not much can be gained from these hidden parts. Only *cristatus* is slightly

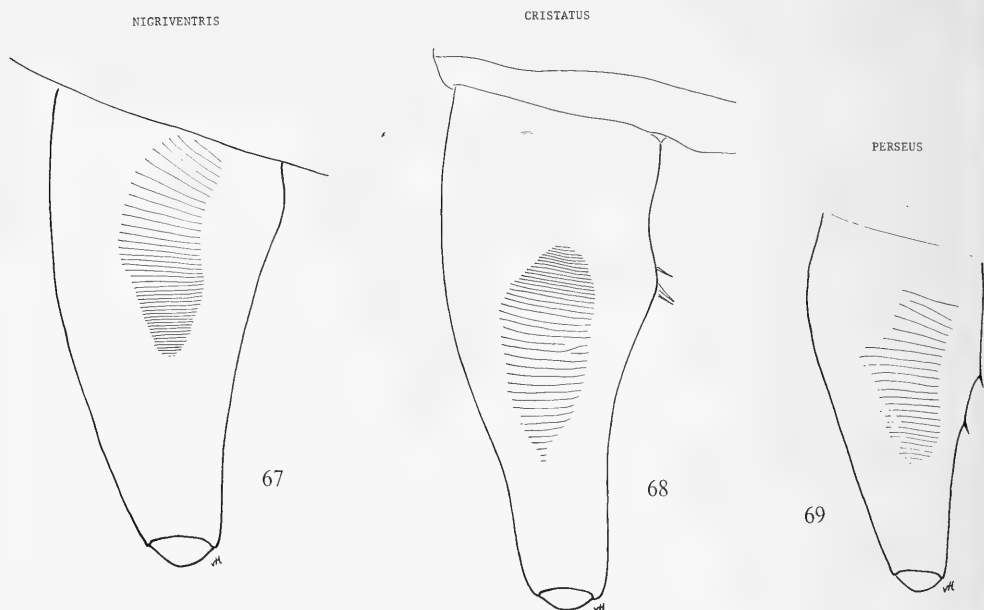


Fig. 67—69. Male chelicerae of *Lepthyphantes* species, showing stridulating files. 67, 68, X 128; 69, X 135

different from the other species. We have observed the scape, therefore, only in the ventral aspect, using the shapes of the basal part of the scape, the visible lateral wings of the inner part, and, of course, the presence or absence of a pit or depression on the basal part.

As to the latter, we may speculate about the functional properties of the pit and depression. From the analysis of the functions of the different elements of the male palp and the epigyne in *L. leprosus* (Ohlert) (Van Helsdingen, 1965), we know that the male palp is firmly anchored on the epigyne by, among others, the male paracymbium. We have already pointed out that in all species with pitted scapes or scapes with depressions the paracymbium of the male palp bears a long tooth. It is not impossible that the large tooth on the paracymbium is functionally correlated with the pit or depression. We must keep in mind though, that the larger tooth on the paracymbium is differently situated in the different species: at the base, and rather at the inside of, the distal branch (*tenebricola*, *jacksoni*, *jacksonoides*), or on the proximal branch (*nigriventris*).

In the male palp, the following characters have been used: dentition of paracymbium, shape of lamella, dentition of basal section of embolus, and possible conspicuous parts of the terminal apophysis. Of these the paracymbial characteristics and the presence of a conspicuous protruding portion of the terminal apophysis have been used for subgroup delimitation. The other characters could not be used for this purpose, but only contributed in a purely typological way to species differentiation.

#### Infra-group relationships.

With the aid of the characters mentioned, we can distinguish certain subgroups

or clusters of species within the *tenuis* group, though it is not possible to divide all species among these clusters. Starting with the species with pit-bearing scapes, we may bring together *nigriventris* (Fig. 49), *camtschaticus* (Fig. 51), and *tenebricola* (Fig. 37).

The scape does not have a pit in the holotype of *camtschaticus*, but it is present in a second specimen from the same region; *camtschaticus* also is suspected to be very close to *nigriventris*, with which it might form a superspecies or polytypic species. However that may be, both have the typical sclerotized posterior margin of the basal part of the scape, a feature we know so well from *tenebricola*. This latter species is now revealed as exceptionally possessing a pitted scape (Fig. 37). The male palps in the two species mentioned here (we do not have a male of *camtschaticus*) have one thing in common, viz., the relatively large, blade-like projecting part of the terminal apophysis (Fig. 36, 47); in both the paracymbium bears a strong tooth, though of different position and in the case of *tenebricola* accompanied by a second tooth. In two other species, *jacksoni* and *jacksonoides*, both male characters are equally present (Fig. 39, 40, 45, 46): the blade-like projecting part of the terminal apophysis, which is even larger here and quite conspicuous, while the paracymbium does have a large tooth, in position comparable to the larger tooth of *tenebricola*. The females of these two species do not have pitted scapes, but both have the rather conspicuous depression near the tip of the exposed basal part of the scape (Fig. 42 and 46). The pit and the depression found in this subgroup might be functionally analogous structures.

A second subgroup is constituted by *L. zimmermanni* and the closely resembling *spiniger* and *floriana*. The epigynes of these three species are hardly different as to the shape of their scapes; all three have proportionally broad posterior median plates. The males have a number of features in common, but as a group they cannot be clearly delimited from the other species. For instance, the basal section of the embolus bears denticles in the three species mentioned, but so it does in *tenuis* and *dremskyi*. Of the latter the female is still unknown, but the female of *tenuis* differs from the *zimmermanni* type (compare Fig. 16 and 24, 30, and 34). *L. herbicola* would, according to the epigyne (Fig. 15), fit in with the *zimmermanni* type, but there are no denticles on the embolus, and the shape of the lamella deviates considerably from what is found there (compare Fig. 13 and 27, 28, and 31).

The teeth on the paracymbium give no clue; they are quite useful for the separation of the species, but relationships cannot be inferred from their numbers, positions, — or absence. We have not succeeded, therefore, in delimiting the *zimmermanni* subgroup more precisely.

We feel that *cristatus* stands quite isolated, forming a possible link with one of the other (natural?) species-groups of the genus; the spinose palpal tibia, the cymbium with its two tubercles, the spatulate lamella, and the strongly sclerotized basal section of the embolus, are not found in any of the other species.

*L. mengei* and *flavipes* seem to be closely related, which might be a mere suggestion because of their small size and the absence of denticles on the embolus, which character also might be correlated with size. *L. perseus* from Iran, described as new in this paper, most likely is related to these two species, even though the

embolic dentition is present. *L. tenebricoloides*, endemic to Madeira and the Canary Islands, rather strongly deviates from the general type; it is larger than most other species, and lacks denticles on the embolus as well as on the paracymbium. *L. drenskyi* and *tenuis* resemble each other very closely in the shape of the lamella and the number of denticles on the basal section of the embolus.

#### Zoogeographical remarks and possible evolutionary lines.

If we correctly have brought together *tenebricola*, *nigriventris*, *camtschaticus*, *jacksoni*, and *jacksonoides* in one natural subgroup, we may try and find an explanation for the present distribution of the species. Of the species under consideration, *tenebricola* certainly has the widest and most central distribution. It occurs in Europe and probably in Asia (Kamtchatka record), as far north as Lapland, as far south as Spain and Italy. In the Alps it reaches an altitude of 2,000 m. In Swedish Lapland it occurs together with *nigriventris*, which may reach much further north and is more adapted to open grassland habitats, while *tenebricola* can be classified as ombrophilous. *L. nigriventris* may have evolved from northern populations of *tenebricola*, which became isolated by the advancing ice-cover in the colder pleistocene periods, and survived in the relatively mild and ice free regions of southern Finland and Siberia (Yenisey region). A similar situation may have occurred in the Alps, where *jacksoni* and *jacksonoides* have a subalpine to alpine distribution (1,300 m and above) and are found in more open vegetation outside the forest. *L. tenebricola* does not occur above 2,000 m and is more or less restricted to the forested areas. Its distribution probably is limited by, or coincides with, the timber-line. The northeast-southwest differentiation into two species may result from the former existence of isolated refugia in the Alps. It is not likely that they represent cases of Nunatak survival, because they are now not of exclusive alpine distribution. We rather think of isolated regions, cut off from the main population of *tenebricola* by chains of glaciated mountains. We know of many of these areas that remained free of ice during the main glaciations (cf. Holdhaus, 1954, map 36).

As pointed out when summarizing the distribution of *L. zimmermanni*, this species has a wide European distribution, which, however, leaves a remarkable hiatus in the eastern Alps and the mountainous regions of the Balkans. All specimens examined from Switzerland came from the western part, mainly the northwestern plain. The species does not occur in the eastern part, nor in Nordtirol, while in Czechoslovakia it is said to be very rare (Buchar, pers. comm). From Hungary there is no record; from Rumania it was erroneously mentioned and the specimens concerned are described as a new species (*floriana*) in this paper. South of the Alps it is known to occur in Italy and northern Yugoslavia. From Bulgaria there is an isolated cave record, but we must not forget, of course, that the European population continues eastward in Poland and the European part of the U.S.S.R. *L. floriana* in our opinion is closely related to *zimmermanni*; so far it is only known from one locality near Bucarest and one in Bulgaria; it may have evolved there from a marginal population of *zimmermanni*.

In the southwest we have a comparable case. Here we find *L. spiniger*, which, if we are not mistaken, is restricted to the Pyrenees, where it inhabits the entrances



of caves and dolines, as well as the litter stratum of pine forest. There are many records of *zimmermanni* from the Pyrenees (in Denis' papers on the spider fauna of that region) and at present the two species are not clearly isolated geographically. It is impossible to speculate here, with our restricted knowledge of the ecological preferences of the two species and of the details of their distributions in the Pyrenees, about the possible influence of the glaciations on the development of these two closely related species.

Only two species have been reported with certainty from Madeira and the Canary Islands, viz., *tenuis* and *tenebricoloides*. According to Schmidt (1975 a and b) both species are subject to more than the usual variation in this archipelago. A specimen of *tenuis* from La Palma was reported (Schmidt, 1975 b) to be much darker than specimens of the mainland populations, a specimen from Gomera appears to be much smaller (Schmidt, 1975 a). Specimens of *tenebricoloides* from Gomera (Schmidt, 1975 a) show differences in the genitalia as well as in size, as compared to the original series from Madeira. It is not surprising that Madeira and the Canary Islands have their own endemic representative (*tenebricoloides*) of the *tenuis* group. This is a well-known phenomenon in many groups of animals, and there are many examples of endemic spiders from these islands. Future investigations may bring to light to what extent the different islands of the archipelago have their own characteristic populations of *tenebricoloides* or related species. Several islands are not yet investigated. As to *tenuis*, we can hardly expect to find much differentiation among the island populations. Again we do not know exactly on which islands the species occurs (so far recorded from Madeira, Gomera, La Palma, and also from the Açores). But *tenuis* apparently is easily dispersed by man, as witness the occurrence in New Zealand, and it is not very likely that different populations have evolved under these conditions. The region certainly is worth special attention.

At the present stage nothing is to be gained from a speculation on the relationships among the remaining species. Our insight in the meaning of the used characters is too superficial. However, progress is helped by a number of factors, which we hope to have made possible through this contribution. In the first place many more records are needed for all the species of this group, with as many particulars on habitats to be recorded as possible. For some species the interest should be focussed on certain regions, viz., the Alps, the Carpathian Mountains, the Balkan Mountains, and the Apennines. There is also no reason why the *tenuis* group should not be represented in the Taunus or Caucasus. The occurrence of *tenuis* in Afghanistan (Denis, 1958) and the recent discovery of *perseus* in Iran clearly show that we may expect representatives of this species-group to occur farther to the east and south. Our knowledge of the faunas of these regions is very poor, certainly as regards the Linyphiidae. We kindly invite the attention of all arachnologists to this interesting group of species.

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## INDEX

(synonyms in italics)

<i>arctica</i> 18	<i>gallicus</i> 8	<i>taczanowskii</i> 19
<i>arcuatus</i> 30	<i>henricae</i> 12	<i>tenebricola</i> 12, 30, 32
<i>aspromontis</i> 17	<i>herbicola</i> 16	<i>tenebricoloides</i> 21
<i>borealis</i> 24	<i>jacksoni</i> 32, 34	<i>tenoides</i> 42
<i>camtschaticus</i> 38	<i>jacksonoides</i> 34	<i>tenuis</i> 17, 42
<i>concinella</i> 8	<i>mengei</i> 8, 12	<i>tomsica</i> 8
<i>concinus</i> 8	<i>nigriventris</i> 34, 36, 42	<i>trucidans</i> 19
<i>cracens</i> 42	<i>pallidiventris</i> 40	<i>zebra</i> 42
<i>cristatus</i> 24, 40	<i>pallidus</i> 40	<i>zebrinus</i> 15
<i>drenskyi</i> 22	<i>perseus</i> 11	<i>zelatus</i> 42
<i>falteronensis</i> 17	<i>pygmaea</i> 15	<i>zibus</i> 42
<i>flavipes</i> 12	<i>sanfilippo</i> 18	<i>zimmermanni</i> 12, 18, 23
<i>floriana</i> 28	<i>spiniger</i> 27	
<i>foliatus</i> 41	<i>suldalensis</i> 42	











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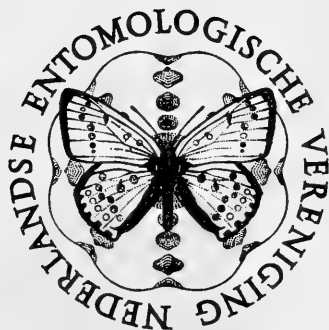
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## INHOUD

J. VAN DER VECHT. — Studies of Oriental Stenogastrinae (Hymenoptera Vespoidea), p. 55—75, fig. 1—49, pl. 1—2.



# STUDIES OF ORIENTAL STENOGASTRINAE (HYMENOPTERA VESPOIDEA)

by

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With 49 text-figures and two plates

This is the third of a series of studies on the Stenogastrinae, an isolated and in many respects particularly interesting group of subsocial wasps. It is also the first paper to deal with the species of the Oriental region, where the group is much more numerous and diverse than in the Papuan subregion. Whereas only 17 species, belonging to two genera, are known from the latter area (Van der Vecht, 1972, 1975), the Oriental region harbours about 50 species belonging to five genera, two of which are new and described in this paper.

It is my intention to discuss the phylogeny and zoogeography of these wasps after the completion of the taxonomic revision. It appears desirable, however, to present at this stage a few notes on the relationships and the status of this group as a whole.

The first author to deal with this question was H. de Saussure (1853, vol. 2: 4), who divided the "Vespides", often called Diploptera<sup>1)</sup> or diplopterous wasps, into "Masariens", "Euméniens" and "Vespiens". Concerning the genus "*Ischnogaster*" (junior objective synonym of *Stenogaster*, the only valid genus-group name available for these wasps before 1914) this author wrote: "Ce genre est, par tous ses caractères, entièrement intermédiaire entre les deux tribus [Euméniens and Vespiens, solitary and social wasps, resp.]. Ses mœurs seules obligent à le classer dans les Guêpes sociales."

Since then there has been little agreement with regard to the question whether the Diploptera should be treated as a single family, embracing three or more subfamilies, or as a superfamily containing two (Börner, 1919) or three families, which in the latter case agree with the groups distinguished by De Saussure. That this question is of some importance in connection with the systematic position of the Stenogastrinae, may be shown by some examples of classifications proposed or used in the past.

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<sup>1)</sup> The name "Diploptera", originally proposed by Latreille, in Cuvier, 1817, Règne Anim. 3: 502, was rejected by De Saussure, because the longitudinal folding of the fore wings when at rest does not occur in certain "Vespides", whereas it is also seen in certain wasps not belonging to this group "(les Leucospidiens, par exemple)" (De Saussure, 1853, vol. 1: XVI). Nevertheless I shall use this term here, because it appears to be the only available unambiguous name for the "Vespides" sensu De Saussure.

Smith (1857) used the term *Diploptera*, gave the three divisions family rank, and placed *Ischnogaster* in the *Vespidae*. Dalla Torre (1894, 1904) followed the classification as given by De Saussure. Bingham (1897) also treated *Ischnogaster* as a member of the family *Vespidae* s. str., but remarked that this genus seems to form "a link between the *Eumenidae* and *Vespidae* both in structure and in habits." Ashmead (1902) placed the three families of *Diploptera*, together with 13 other families of *Hymenoptera* (including *Trigonalidae*, *Bethylidae*, *Chrysididae*, *Pompilidae*, *Mutillidae*, etc.), in one superfamily *Vespoidea*; he created a new subfamily *Ischnogasterinae*, containing the African genus *Ischnogasteroides* Magretti<sup>1)</sup> in addition to the type-genus, and placed this in the *Eumenidae*.

Bequaert (1918) and Bradley (1922) provided a classification in which all the diplopterous wasps are regarded as a single family (*Vespidae*), subdivided in 10 or 11 subfamilies, 2 or 3 of these corresponding with the former family *Masaridae*, 3 with the *Eumenidae*, and 4 with the *Vespidae*. By placing the *Stenogastrinae* in between the two last mentioned groups, the problem of the relationships of this subfamily remains completely open, since no choice between the viewpoints of De Saussure and Ashmead is necessary.

Börner (1919) divided the *Diploptera*, which he called "*Vespina*", into two families, each with two subfamilies: *Vespidae* with *Vespinae* and *Eumeninae*, and *Masaridae* with *Masarinae* and *Celonitinae*; he could not examine *Ischnogaster* and *Ischnogasteroides*, which he regarded as social wasps, but suggested that these might be closely related to the *Eumeninae*.

In more recent literature, the term *Vespoidea* is either used for a group of several families, including the *Diploptera* (Imms, 1925 and later editions; Essig, 1942; Bradley, 1958; Brothers, 1975), or exclusively for the *Diploptera*. In the latter case, the superfamily may either contain one family *Vespidae* with several subfamilies (Brues & Melander, 1932; Muesebeck c.s., 1951) or the usual three families (Richards, 1962). The latter classification is here of particular interest, because it requires an answer to the question of the affinities of the *Stenogastrinae*. Richards decided to place them again in the family *Vespidae* s. str. (social wasps), although it is evident from his enumeration of the characters of this group (l. c.: 22), that they take a very isolated position there.

Since then, the further study of these wasps has brought to light that the differences between the *Stenogastrinae* and the other social wasps (*Polistinae* and *Vespinae*) are considerably greater than would appear from this enumeration. Richards himself has already pointed out that the *Stenogastrinae* differ from all other *Vespoidea* in having the small subcircular pronotal lobe at a point almost halfway between the tegula and the fore coxa (Richards, 1972). This character, together with some others (long pointed clypeus and long narrow mandibles lying alongside it) led him to remark that the *Stenogastrinae* are very different from other social wasps and might even have evolved independently from some *Eumenes*-like, solitary ancestor (Richards, 1971).

Spradbery (1975: 317) compared the *Stenogastrinae* with the *Eumenidae* and

<sup>1)</sup> This is a small group of solitary wasps which are structurally very close to *Eumenes*; Ashmead's error was corrected by Meade-Waldo (1913: 54).

other Vespidae for 17 "biological characteristics"<sup>1)</sup> and concluded that "the Stenogastrinae exhibit a number of unique features which suggest that they originated from an early vespoid ancestor and diversified in the specialized environment of the deeply shaded rain forest."

In the course of my studies of the Stenogastrinae some other characters have been noticed which lend support to these ideas.

(1) Glossa and paraglossa do not have sclerotized pads (acroglossal buttons) at their tips<sup>2)</sup>. The Stenogastrinae agree in this respect with certain primitive Masaridae. The absence of such pads in the few Stenogastrinae known to him was already noted by De Saussure (1852a: 22; 1853, vol. 2: 3, footnote 1).

(2) The occipital keel runs down ventrally to meet the hypostoma close to its base (see Richards, 1962: 11, and this paper, Fig. 1 and 2). This condition is not found in the Polistinae and Vespinae. But the keel forks in several Zethinae<sup>3)</sup> and in the South American genus *Plagiolabra*, one branch going to the hypostomal keel and one to the mandible base. In some American *Zethus* species (*Z. cinerascens* Saussure, *cristatus* Fox, *spinipes* Say, and probably others) the mandibular branch is almost or entirely absent, and the situation is then very similar to that found in the Stenogastrinae.

(3) Mandibles projecting beyond tip of clypeus, at least in ♀ of some genera distinctly crossing when at rest (Van der Vecht, 1972, Fig. 1 and 14), tridentate in ♀, often more or less reduced in ♂ (in Eumenidae and Vespidae the mandibles of ♀ usually have 4 or 5 teeth).

(4) Clypeus of ♀ pointed at apex (in ♂ sometimes rounded), differing from clypeus of many Polistinae (♀) in absence of projecting lateral angles of anterior margin.

(5) Antennal sockets far apart, close to centre of eye-emargination, separated from upper margin of clypeus (often only weakly indicated) by long (*Liostenogaster*) to very long (*Stenogaster*) supraclypeal area.

(6) Apart from some characters already mentioned previously (see Richards, 1962), the wings of the Stenogastrinae are distinguished by (a) the shape of the marginal cell (marginal vein bluntly angled at end of first abscissa, where *r* meets *Rs*, and then running in an almost straight line to wing margin) and (b) by the presence of only two closed cells in the hind wing, the costa being more or less distinctly reduced distally. The row of hamuli is often once or twice interrupted.

(7) The male genitalia, particularly aedeagus and volsella, are rather different from those of other diplopterous wasps, but are perhaps most similar to those of certain Zethinae.

(8) The gaster (metasoma) of the pupa is strongly bent at the articulation of

<sup>1)</sup> This author has overlooked (Table 2, line 2) that Raphiglossinae and Zethinae<sup>3)</sup> are known to use plant materials for nest construction.

<sup>2)</sup> The statement about the occurrence of acroglossal buttons in the Vespidae (Richards, 1962: 22) should be corrected by inserting "(except in the Stenogastrinae)" after the word "present".

<sup>3)</sup> Richards (1962: 4) and Bohart & Stange (1965) have used the name Discoeliinae Thomson, 1874, for this subfamily, but in accordance with article 11 (e) of the Code the name Zethinae Saussure, 1855, originally proposed as "Zethites" for a group containing the genera *Calligaster*, *Zethus* and *Discoelius*, has priority.

segments 1 (petiole) and 2. This phenomenon does not occur in the Polistinae with petiolate abdomen (the body of the pupa of *Belonogaster*, for example, is perfectly straight), but it is well known from several Eumenini (example: photograph of pupae of *Delta emarginatum* (L.) in Bonelli, 1973). Less attention has been given to the pupae of the Zethinae, the other Eumenid group of cell-builders with petiolate gaster. Except for a figure of the pupa of *Calligaster williamsi* Bequaert ("Zethus cyanopterus") in Williams' paper on the biology of Philippine wasps (1919: 162, Fig. 94), which clearly shows "its bent attitude", I looked in vain for information on this subject in some literature directly at hand. The only pupa figured in Bohart & Stange's (1965) revision of American *Zethus* seems to have the gaster very slightly curved, but the drawing is small and rather schematic.

Fortunately I could study the pupae from nests of some *Zethus* spp. collected in Surinam by Mr. G. van Vreden (*Z. prominens* Fox, no. 133 Mus. Leiden, and *Z. miniatus* Sauss., no. 123) and by myself (*Z. binodis* (F.), no. 226). The first-mentioned species is an interesting exception to the rule that the members of the subgenus *Zethus* nest in insect burrows in twigs or wood; the nest found by Van Vreden at Afobaka in a hollow tree is an irregular cluster of more than 30 cells, each measuring about  $3 \times 1.5$  cm, built of vegetable material consisting mainly of fragments of parts of inflorescences of an unidentified plant species, pasted together with a resinous substance. A pupa from this nest has the gaster sharply bent, the angle between the axis of the petiole and that of the remaining segments being about  $70^\circ$ . In a pupa of *Z. (Zethoides) miniatus* this angle is about  $50^\circ$ , and in one of *Z. binodis*, which belongs to the same subgenus but has a relatively longer petiole, it is only  $35^\circ$ . The few available figures seem to suggest that the angle becomes sharper with increasing length of the petiole, but much more information is required for a reliable conclusion. It would be particularly interesting to have data on the pupae of species which resemble Stenogastrine wasps more closely in petiolar length, such as certain members of the groups of *Z. fuscus* (Perty), *Z. strigosus* Saussure, and *Z. montezuma* Saussure.

However, it is already possible at this stage to establish that the pupae of certain Zethinae are very similar to pupae of Stenogastrinae, as figured by Iwata (1967, *Parischnogaster* spp., Figs. 6-9, angle of gaster  $25-45^\circ$ ) and Spradbery (1975, *Stenogaster concinna*, Fig. 9, angle about  $50^\circ$ ).

Some provisional conclusions from the data now available are:

(a) The Stenogastrinae are so different from the Polistinae and the Vespinae, both in morphological and in ethological characters, that a taxon consisting of these three groups cannot be regarded as monophyletic.

(b) The Stenogastrinae are likely to have evolved from a solitary cell-building ancestor with elongate gastral petiole.

(c) Several characters, including those mentioned above under 2, 3, 7 and 8, suggest that this ancestor was more closely related to the Zethinae than to the Eumenini.

(d) Data on geographic distribution are not in contradiction with this theory. The present distribution and diversity of the Zethinae in the Old World indicate that this subfamily has been represented here long enough to allow for the radiation of the Stenogastrinae in the Indo-Australian area.



The consequences of these conclusions for the classification of the Diploptera should be further studied in the framework of a revision of this group by modern methods, for which Brothers' recent study of the Aculeate Hymenoptera (1975) may serve as an example. Meanwhile, if one accepts the subdivision of the Diploptera into three (or more) families, a choice must be made whether to treat the Stenogastrinae as a separate family or as a subfamily of the Eumenidae. In my opinion the latter solution would then be preferable. However, I agree with Richards (in litt., July 1976) that the best course might perhaps be to treat the diplopterous wasps again as one family with several subfamilies, approximately those listed on p. 4 of his revision of the Masaridae.

#### KEY TO THE GENERA OF THE STENOGASTRINAE

1. Propodeum posteriorly with a very short constricted neck; its extreme edge slightly raised, seen in profile as forming a minute tooth above the gastral muscle. Head (excluding clypeus and mandibles) subcircular, at most moderately wider than high (13 : 10). Mandibles of ♂ without teeth, rather abruptly narrowed from the middle, the apex curved and acute. Clypeus of ♂ flattened to concave. Posterior margin of hind wing of ♂ normal. — New Guinea and some neighbouring islands . . . . . *Stenogaster* Guérin
- Posterior edge of propodeum not raised. Head (excluding clypeus and mandibles) as a rule much wider than high. Mandibles of ♂, if without teeth, not abruptly narrowed. Clypeus of ♂ more or less convex. . . . . 2
2. All segments of maxillary palpi about equally long (if segment 2 is twice as long as 3, gastral segment 2 is not distinctly petiolate and occipital carina ends below at short distance from hypostomal carina). — Oriental Region. . . . . 3
- Segment 2 of maxillary palpi more than twice as long as 3. . . . . 6
3. Mesoscutum shining, with sharply impressed prescutal sutures, running on outer side of anterior yellow marks backwards to level of tegulae. Head broadly oval, width about 1.4 to 1.5 times height of eye. Spiracles of gastral segment 2 clearly visible in dorsal aspect (Fig. 30). — Malaya, Sumatra, Borneo, Palawan, and Java. . . . . *Metischnogaster* gen. nov.
- Mesoscutum without prescutal sutures, or with ill-defined and shallow sutures on dull mesoscutum (in group of *Parischnogaster*). Spiracles of gastral segment 2 not visible in dorsal aspect . . . . . 4
4. Occipital carina joins hypostomal carina near base of proboscideal fossa (Fig. 2). Gaster petiole long, more than 1.5 times length of thorax; segment 2 as a rule distinctly petiolate. Antennae rather strongly swollen beyond segment 6 or 7. Parameral spine of male genitalia dilated, forming a broad lamella with short apical spine. . . . . 5
- Occipital carina ending at short distance from hypostomal carina (Fig. 1). Gaster petiole less than 1.5 times length of thorax; segment 2 gradually narrowing towards base, not petiolate. Antennae only slightly clavate. Parameral spine normal. (Mid tarsi of ♂ not dilated, symmetrical.) — Burma and Thailand to Celebes and Java. . . . . *Liostenogaster* Van der Vecht

5. Clypeus longer than shortest interocular distance (Fig. 38 and 43). Mouthparts long, protruding beyond tip of clypeus over a distance well exceeding length of clypeus. Mid tarsi of ♂ very slender, symmetrical. — Borneo and Sumatra. . . . . *Holischnogaster* gen. nov.
- Clypeus rarely a little longer than shortest interocular distance. Mouthparts short, protruding less far beyond tip of clypeus. Mid tarsi of ♂ partly dilated, at least one segment asymmetrical. — India to Celebes. . . . . *Parischnogaster* Schulthess
6. Scutellum strongly convex, with sharp median carina. Mandibles of ♂ as a rule without teeth on inner side or, rarely (in species from continental S. E. Asia), with one very blunt and faintly indicated tooth. Proximal part of hind wing of ♂ with opaque greyish or brownish seam at posterior margin. Length to apex of second gastral segment exceeding 16 mm. — Southern India to Celebes. . . . . *Eustenogaster* Van der Vecht
- Scutellum more or less convex, but without median carina. Mandibles of ♂ with at least one distinct tooth on inner side. Hind wing of ♂ without dark seam. Length to apex of second gastral segment at most 14 mm. — New Guinea and some neighbouring islands. . . . . *Anischnogaster* Van der Vecht

**Metischnogaster** gen. nov.

(Fig. 2-37, Pl. 1, 2)

Head, including clypeus, wider than high (about 11 : 10 in ♀, 12.3 : 10 in ♂), and distinctly wider than thorax; width of head: height of eye = 14.5-15 : 10 in ♀ and 15.5-16 : 10 in ♂). Clypeus moderately convex, shining and sparsely punctate (♀) or practically impunctate (♂); anterior portion bluntly keeled in the middle and ending in a sharp point. Mandibles short, tridentate in ♀, bidentate in ♂. Segment 2 of maxillary palpi not lengthened; segment 1 of labial palpi long, but shorter than 2-4 together. Antennae moderately clavate, segment 10 less than twice as wide as segment 4; flagellum flattened and ventrally yellowish-white in ♂. Vertex with impressed median line (sometimes partly indistinct) between anterior ocellus and occipital carina.

Thoracic complex small, egg-shaped, and widest below tegulae; mesoscutum with distinct prescutal sutures, running from anterior margin along outer side of yellow marks to level of tegulae; parapsidal furrows starting a little in front of anterior tangent of both tegulae, before reaching posterior margin of mesoscutum a little dilated and bordered on outer side by fine carina. Scutellum moderately convex, faintly carinate mid-anteriorly. Metanotum rather strongly convex in profile. Propodeum shining, on posterior surface with oblique striation, transition between posterodorsal and lateral areas rounded; median line impressed, most distinctly at base and apex, and near the middle very slightly raised; valvulae strongly reduced. — In the ♂ the greater part of mesepisternum, metapleura and sides of propodeum take part in the formation of a dull, densely pubescent, sunken area. This area is bordered posteriorly by a sharp and more or less arcuate carina, situated between posterior margin of metapleura, just below propodeal spiracle, and apical margin of propodeum, close to posterior end of valvula.

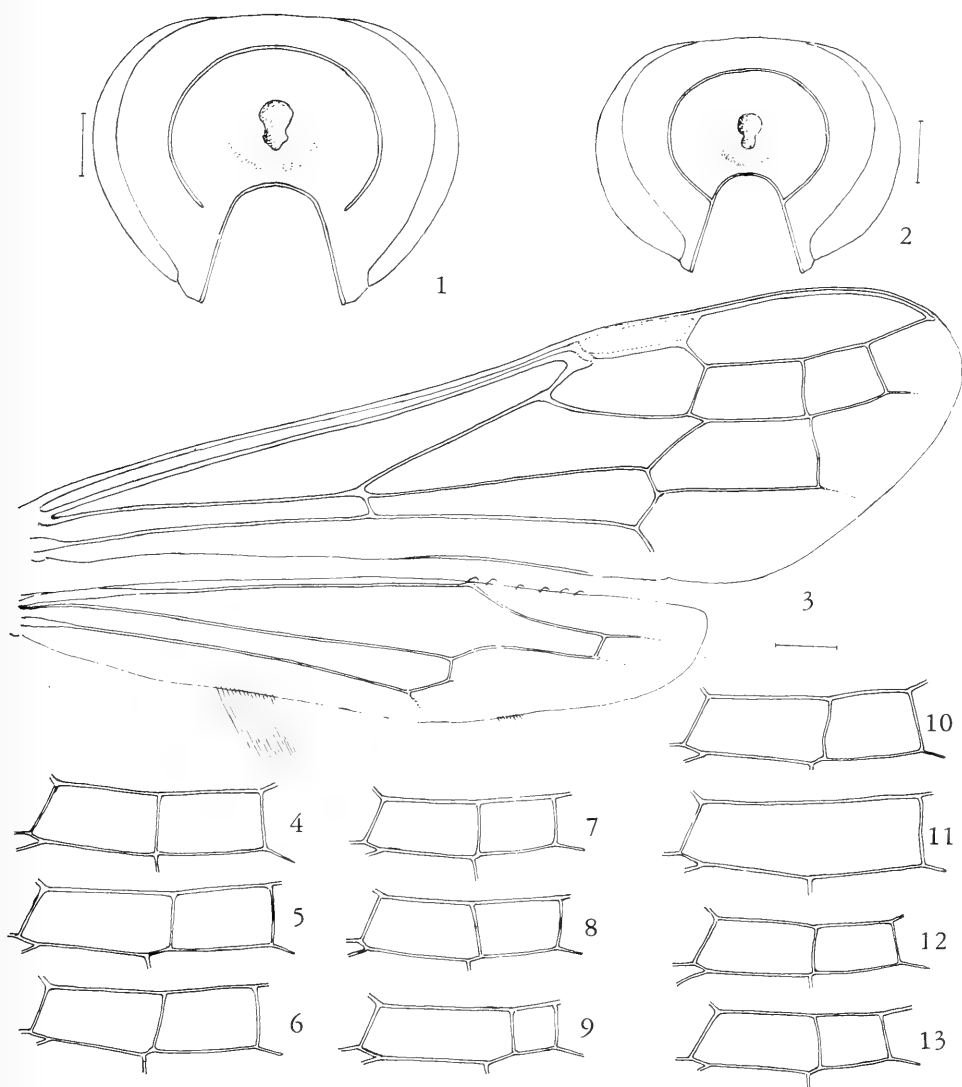


Fig. 1—2. Rear view of head (mouthparts and clypeus omitted). 1, *Liostenogaster nitidipennis* (Saussure) ♀, Borneo; 2, *Metischnogaster drewseni* (Saussure) ♀, Java. Fig. 3. Wings of *Metischnogaster drewseni* (Saussure) ♂, Java. Fig. 4—13. Submarginal cells 2 and 3 of right fore wing of *Metischnogaster*. 4—6, *M. cilipennis* (Smith) ♀, Malaya; 7—9, same, ♂, Malaya and Borneo (no. 9). 10, 11, *M. drewseni* (Saussure) ♀, Java (in 11 transverse vein absent in both wings); 12, 13, same, ♂, Java and Billiton. Scale lines represent 0.5 mm.

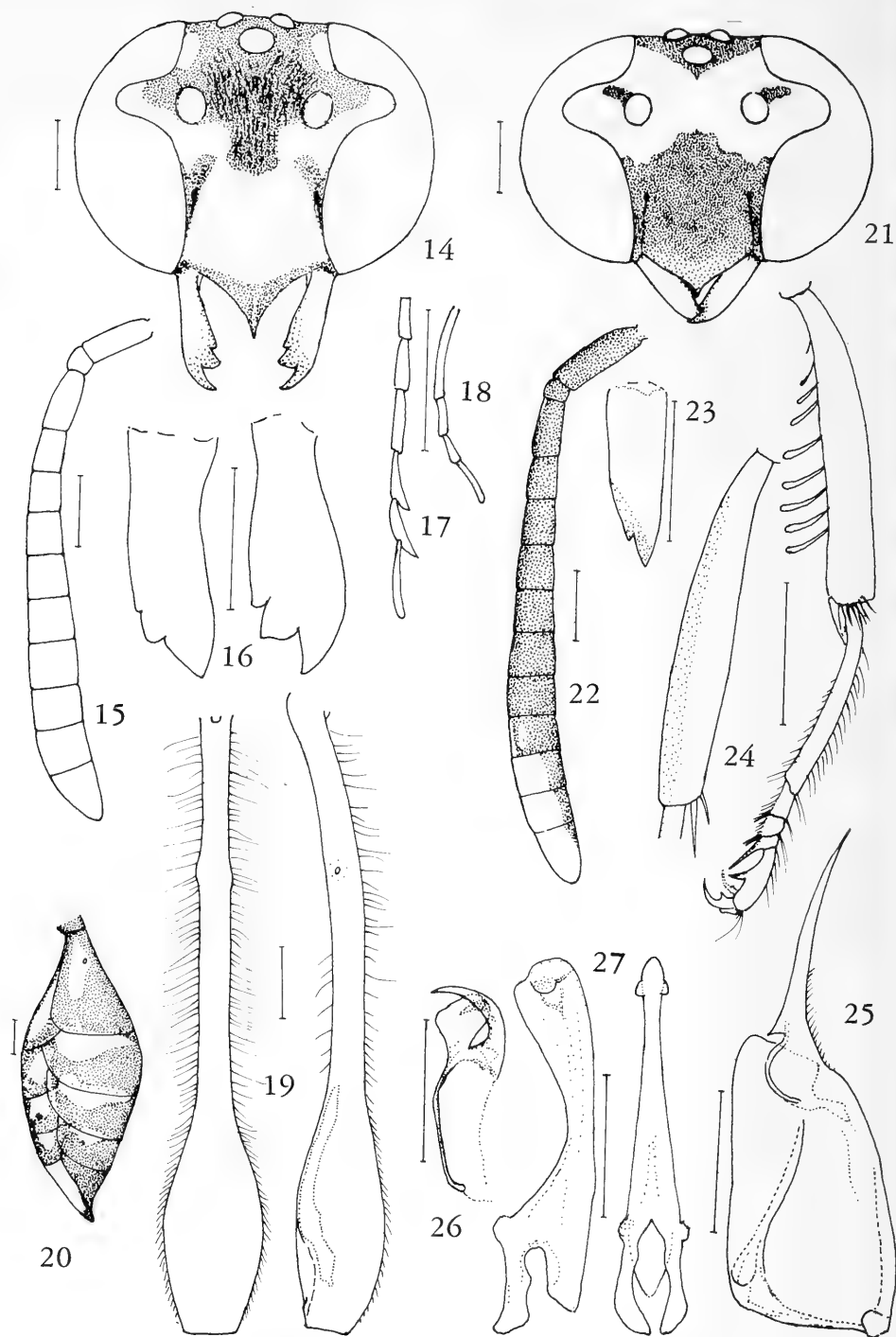


Fig. 14—20. *Metischnogaster cilipennis* (Smith) ♀, Malaya. 14, head; 15, antenna; 16, mandible, lateral and laterofrontal views; 17, maxillary palp; 18, labial palp; 19, gastral petiole, dorsal and lateral views; 20, gastral segments 2—6, lateral view. Fig. 21—27. *Metischnogaster cilipennis* (Smith) ♂, Malaya. 21, head; 22, antenna; 23, left mandible, lateral view; 24, fore tibia and tarsus, and mid tibia; 25, paramere; 26, volsella; 27, aedeagus, lateral and dorsal views. Scale lines represent 0.5 mm.

Legs slender, bearing numerous scattered long hairs, notably on coxae II and III, on trochanters, at base of ventral side of femora and on outer side of tibiae and tarsi; tibiae I of ♀ on inner side with irregular row of short spines. In ♂ tibiae I armed with a row of peculiar, slightly curved, spatulate setae (Fig. 24); tarsi II symmetrical; segment 4 of tarsi I and II produced beneath into a long spine, segment 5 with a shorter spine on ventral surface (Fig. 24 and 34).

Wings (Fig. 3-13) rather variable within the species as regards shape of second and third submarginal cells and course of second recurrent vein, the latter sometimes received in the third submarginal cell; sides of stigma almost parallel; hind wing narrow, with posterior fringe of anal cell in ♀ slightly lengthened, in ♂ very long.

Gastral petiole (Fig. 19 and 29) slender, greater part subcylindrical, somewhat asymmetrically swollen at spiracles, apical two-fifths swollen into elongate bulbus which is about 3.3 to 3.6 times as wide as the anterior part; tergite and sternite almost completely fused, the suture separating them visible only on apical two-thirds of ventral side of bulbus. Second segment (Fig. 20 and 30) at most shortly petiolate; spiracles close to base on dorsal surface. Terminal segment conical (♀) or with flattened sternite (♂). Male genitalia (Fig. 25-27, 35-37): parameral spine long, with sharp tooth at base; volsellar digitus sickle-shaped; aedeagus compressed, posterior part much higher than wide and near apex on each side with small lamellar or spiniform process, ventral processes rudimentary.

Length to apex of second gastral segment: 9-11 mm.

Type-species: *Ichnogaster cilipennis* Smith, 1857.

Distribution. — Malay Peninsula, Sumatra, Borneo, and Java.

Bionomics. — Our present knowledge of the life history of the two known species (possibly the only ones existing) is entirely due to investigations made in Malaya by H. T. Pagden (1958, 1962). The first paper deals with several *Stenogastrinae* and contains, in addition to a description and some figures of the peculiar characters of the ♂ of "*Stenogaster*" *cilipennis*, a note on the habit of hovering of these males and a drawing from a photograph of "the first nest ever found" of this species. A closely related species, supposed to be undescribed, but later identified as *drewseni*, was briefly mentioned. Further data are given in the second paper, which is exclusively devoted to the habits of these two species.

The nest of *M. cilipennis* (Pl. 1) consists of an almost straight row of rarely more than a dozen cylindrical cells, the first of which is usually attached to a hanging thread of the fungus *Marasmius* (horse-hair blight) or to hanging rootlets; each following cell is then built in a direct line with the preceding one, the openings of the cells being directed sideward. The nests are protected by one or more "ant guards", constructed of the same material as the cells (probably made sticky); they are difficult to find, being built in protected places, apparently often under overhanging banks (above or close to water) and screened by vegetation. The nests of the two species were found to be so similar, that no differences could be detected. The construction of the nest takes a long time, one nest of *M. drewseni* was observed to grow from 5 to 10 cells in about 4 months. Pagden noted that at least two females and two males were present on this nest when the sixth cell was about three-quarters complete. There is some evidence that the females of *M.*

*cilipennis* collect food by hovering in front of spider's webs from which they pick small Diptera. The peculiar habit of hovering and patrolling in favoured shady places was observed in the males of both species (Pl. 2).

## KEY TO SPECIES OF METISCHNOGASTER

### Females

1. Interocular part of clypeus almost entirely yellow; yellow marks at inner orbits coalescent with yellow clypeus or (in specimens from Borneo) separated. Tibiae III yellow on outer side. Anterior (dark) part of dorsal surface of propodeum indistinctly striate. Gastral petiole (Fig. 19) shorter in relation to width of bulbus, with numerous long, outstanding, hairs on cylindrical part and short hairs on bulbus. Gastral tergites 3 and 4 with basal yellow band (more or less hidden under preceding tergites), which is interrupted medially and dilated laterally . . . . . *cilipennis* (Smith)
- Interocular part of clypeus yellow with broad, dark brown, median stripe (Fig. 28); yellow marks at inner orbits separated from those on clypeus. Tibiae III with short yellow line on outer side at base (absent in specimens from Java). Dorsal surface of propodeum entirely obliquely striate. Gastral petiole (Fig. 29) longer and less hairy, the short hairs on bulbus much sparser. Gastral tergites 3 and 4 each with two widely separated yellow spots. . . . . *drawseni* (Saussure)

### Males

1. Terminal three or four antennal segments mainly whitish dorsally (note that the antennae may be more or less twisted). Markings of scutellum, metanotum and propodeum ivory-white, the latter mark well separated from the carina bordering the pubescent area. Metapleura without yellow spot. Gastral tergite 2 as a rule without yellow spot beneath spiracle. Aedeagus on each side with small subapical lamellar projection (Fig. 27) . . . . . *cilipennis* (Smith)
- Terminal six or seven antennal segments (five in ♂ from Palawan) mainly, or at least partly, whitish dorsally. Markings of scutellum, metanotum and propodeum yellow (like the other thoracic markings), the last mentioned mark abruptly dilated at apex, forming a band along posterior margin of shiny part of propodeum. Metapleura with yellow spot beneath base of hind wing (not always distinct). Gastral tergite 2 with elongate yellow spot beneath spiracle. Aedeagus with small subapical tooth on each side (Fig. 37) . . . . . *drawseni* (Saussure)

### **Metischnogaster cilipennis** (Smith) (Fig. 4-9, 14-27)

*Ischnogaster cilipennis* Smith, 1857, Cat. Hym. Brit. Mus. 5: 92, ♂ — "Malacca (Mount Ophir)", leg. A. Wallace (lectotype by present designation BM, no. 18.713); 1858, J. Proc. Linn. Soc. Zool. 2: 113 (Sarawak, Borneo); 1871, J. Proc. Linn. Soc. Zool. 11: 378 (cat.). — Dalla Torre, 1894, Cat. Hym. 9:

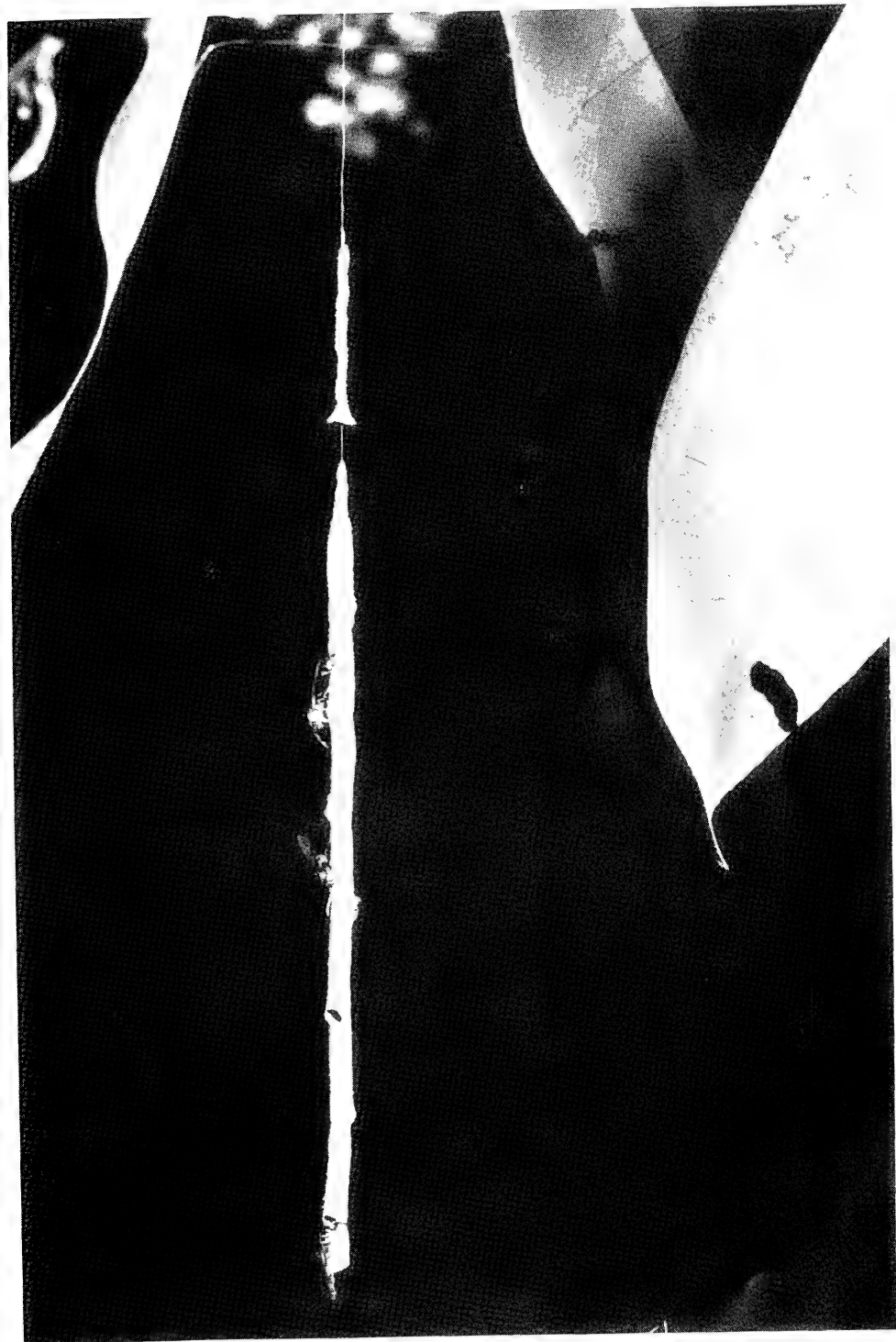


Plate 1. Nest of *Metischnogaster cilipennis* (Smith), built on thread of horse-hair fungus (*Marasmius*),  $7\frac{1}{2}$  cells below "ant guard", with two female wasps (on cells 2 and 8) and one male (slightly reduced).  
Malaya, Selangor, Ampang Reservoir, 9 May 1960.

Photograph by H. T. Pagden.

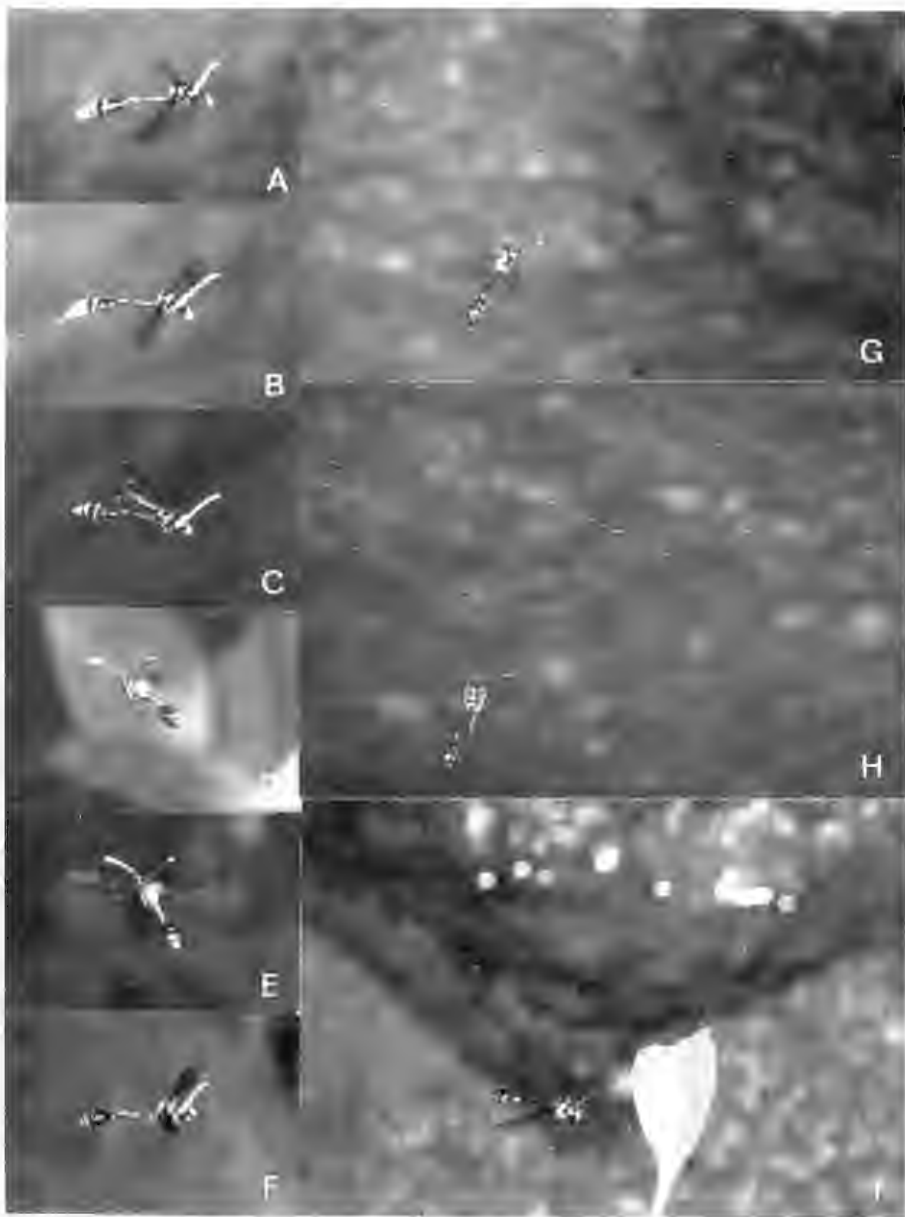


Plate 2. Left: hovering males of *Metischnogaster cilipennis* (Smith) (A-E) and *M. drewseni* (Saussure) (F); right: females of *M. cilipennis* searching at spider webs (slightly enlarged). Penang, Sungei Batu Feringgi, 11 April 1960.  
Photographs by H. T. Pagden.



113 (cat.); 1904, *Genera Insect.* 19: 83 (cat.). — Schulthess, 1914, *Zool. Jb. Syst.* 37: 255 (in subgenus *Parischnogaster*).

*Parischnogaster cilipennis*; Schulthess, 1927, *Supplta ent.* 16: 87 (cat.).

*Stenogaster cilipennis*; Dover, 1931, *J. fed. Malay St. Mus.* 16: 256 (Perak and Pahang, Malaya). — Pagden, 1958, *Malay. Nat. J.* 12: 141—145, Fig. 21, 22 (characters; bionomics in Malaya); 1962, *Malay. Nat. J.* 16: 95-102, Pl. 13-15 (bionomics in Penang). — Yoshikawa c. s., 1969, *Nature & Life in S. E. Asia* 6: Pl. 34, 35 (nests, Malaya).

Note: for *Ischnogaster cilipennis* sensu Buysson, 1909, see under *M. drewseni* (Saussure).

Material. — Malaya: Perak, 2 ♂ Jor Camp, 2000 ft, 22 Aug. 1922, E. Seimund (BM); Pahang, 3 ♂ Sungei Tahang, 23 Nov. 1922, H. M. Pendlebury (BM); Selangor, Ampang Reservoir, 5 ♀ (nrs. 981-983, 985, 987) and 1 ♂ (980) ex nest, 9 July 1947, 2 ♀ (1091, 1092) and 4 ♂ (1093-1096) ex nest, 5 Oct. 1947, H. T. Pagden (BM, 3 ♀ 2 ♂ ML); do., 1 ♀ 29 Febr. 1948, ex nest, *Comm. Inst. Ent.* no. 10909, with note "see also nest sent 28.4.48, G. N." (BM); Selangor, 3 ♂ 40 km N. of Kuala Lumpur, 16 Sept. 1960, J. L. Gressitt (BISH, 1 ♂ ML), 1 ♂ Temple Park near Kuala Lumpur, 14 June 1973, D. K. McAlpine (AMS); Malacca, 3 ♂ Mt. Ophir (BM, lectotype and paralectotype; OUM, paralectotype).

Sumatra: N. E. Sumatra, 1 ♂ Serdang, Tandjong Morawa, Dr. B. Hagen (ML).

Borneo: Sarawak, 1 ♀ "Sar.", leg. A. Wallace (OUM), 1 ♂ Lundu, 21 Oct. 1909 (MCZ); East Borneo, 1 ♀ Tabang, Bengen River, 125 m, 5 Sept. 1956, 1 ♂ Balikpapan, Mentawir River, Oct. 1950, A. M. R. Wegner (ML).

## Female

Head (Fig. 14), including clypeus, wider than long, preocular part of clypeus about 1/5 of total length; interocular distance on vertex slightly longer than at clypeus. Interocular part of clypeus in profile moderately convex, anterior part almost straight; the latter with blunt median carina ending in a sharp point. Mandibles: Fig. 16. Segment 2 of maxillary palpi slightly shorter than each of the following segments, segments 4 and 5 produced beyond the implantation of the next segment (Fig. 17). Segment 1 of labial palpi shorter than 2-4 together (4 : 5). Antennal segment 3 slightly shorter than scape (7 : 8), segment 10 less than twice as wide as segment 4. Ocelli large, transverse diameter of anterior one about 4/7 of its distance from inner orbit, posterior ocelli smaller and almost circular, farther from eyes than from each other (11 : 9), latter distance shorter than their diameter (9 : 10).

Gastral petiole (Fig. 19) slightly more than 1.5 times as long as thorax, its length about 6 times greatest width of bulbus.

Clypeus shining, slightly roughened medially, with scattered, superficial, setigerous punctures. Front and supraclypeal area less shining, longitudinally punctate-rugose, with short and low keel between and slightly in front of antennal sockets. Vertex shining, with some shallow and ill-defined punctures. Thorax generally smooth and shining, upper part of mesepisternum and lower part of metapleura very finely and superficially striate or punctate-striate; mesoscutum polished, with some scattered, setigerous, micropunctures. Dorsal surface of propodeum finely obliquely striate, basally the striation partly obsolete, the striae

meeting under a sharp angle medially. Gastral segments shining, almost smooth; a fine microsculpture is most distinct on the third and following segments.

Short to moderately long hairs are present on most parts of the body, those on the face have in certain lights a golden shine; longer hairs are most conspicuous on mandibles, anterior part of clypeus, vertex, metanotum, propodeum, proximal part of legs, cylindrical part of gastral petiole and on hind margin of gastral sternites.

Ground colour of head and thorax dark brown to black, gaster and legs slightly paler; bright yellow markings: on face and mandibles as shown in Fig. 14, most of pronotal collar, interrupted band at hind margin of pronotum (bluntly angular on outer side at shoulders), two elongate spots at anterior margin of mesoscutum and two spots close to its posterior margin, two spots on scutellum, two on mesepisternum (one close to base of fore wing, a lunate one below transverse suture), broad band on metanotum (incised posteriorly), large spot on upper part of metapleura, about posterior half of propodeum, coxae almost entirely, greater part of femora I, distal half or more of II and tip of III, tibiae I and II (except for brown stripe on inner side), dorsal stripe on tibiae III, basitarsus I above, short line on basitarsus II (sometimes lacking), curved stripe at lateral margin of tergal part of petiolar bulbus and some elongate spots on sternal part, more or less variable markings on postpetiolar part of gaster (Fig. 20). Wings subhyaline, strongly iridescent, veins and stigma dark brown.

Length (h. + th. + t. 1 + 2): 9.5-11 mm.

### Male

Head (Fig. 21) relatively wider than in the ♀, anterior portion of clypeus shorter, mandibles weaker, bidentate, and with sharper teeth. Antennae flattened, apparently with rather soft underside (often shrivelled in dried specimens), scape relatively longer than in ♀ (about 1.5 times as long as segment 3). Pubescent area on sides of thorax large, including entire mesepimeron. Femora I strongly curved in frontal view, tibiae I with row of spatulate setae (Fig. 24), tibiae II compressed and dilated (Fig. 24), outer (anterior) surface bare, flattened and rather dull through fine sculpture, tarsal segments 1-3 of fore and mid legs with two rather long apical spines, 4 produced into a single long spine and 5 with shorter spine on ventral side (Fig. 24); scattered hairs on tarsi much longer than in ♀. Terminal gastral sternite flattened, truncate at apex. Genitalia: Fig. 25-27.

Colour pattern conspicuously different from that of ♀. Face dark brown (apex of clypeus paler) with broad, irregular, transverse yellow band (Fig. 21); ventral side of antennal scape and segment 2 polished and ivory-white, flagellum pale yellow beneath (on inner side when directed downwards), segments 11-13 mainly yellowish white above (Fig. 22) (in ♂ from Sumatra segments 10-13). Thorax without spots on lower part of mesepisternum and on metapleura; markings on scutellum, metanotum and dorsal surface of propodeum together forming one broad, longitudinal, subrectangular, ivory-white stripe. Coxae II and III partly brownish, femora brown with yellow mark at apex, tibiae I and II slightly darker than in ♀, III brown with at most a short yellow line at base; tarsi brown, dorsal surface of basitarsus I yellowish. Gastral petiole dorsally with whitish stripe, dilated on bulbus (anterior part may be partly indistinct or absent); no lateral

marks on bulbus and on tergite 2; 3 slightly paler anteriorly, 4 with basal yellow band, dilated in the middle and at the sides, 5 with wider basal whitish band, narrowed laterally, 6 mainly whitish, the dark posterior margin covering less than one-third of the tergite, sternites 2-6 pale brown, each with two yellow spots; terminal segment entirely whitish.

Length (h. + th. + t. 1 + 2): 9-10 mm.

### ***Metischnogaster drewseni* (Saussure) (Fig. 2, 3, 10-13, 28-37)**

*Ischnogaster drewseni* Saussure, 1857, *Annls Soc. ent. France* (3) 5: 315, ♂ — “Poulo-Pinang, Ile de l'Archipel Indien”, leg. Drewsen (MHNG). — Smith, 1858, *J. Proc. Linn. Soc. Zool.* 2: 113 (Sarawak, Borneo; Mt. Ophir, Malaya). — Dalla Torre, 1894, *Cat. Hym.* 9: 113 (cat.); 1904, *Genera Insect.* 19: 83 (cat.). — Buysson, 1909, *Annali Mus. civ. Stor. nat. Genova* 44: 312 (syn. of *Ischnogaster cilipennis*). — Schulthess, 1927, *Supplta ent.* 16: 87 (cat., in synonymy of *Parischnogaster cilipennis* (Smith)).

*Ischnogaster cilipennis*; Buysson, 1909, *Annali Mus. civ. Stor. nat. Genova* 44: 312 (description of ♀, Lelemboli, Nias) [misidentification].

*Stenogaster drewseni*; Pagden, 1962, *Malay. Nat. J.* 16: 95-102, Pl. 13 (bionomics in Penang).

**Material.** — Malaya: Kedah, 2 ♂ near Jitra Catchment Area, 6 and 9 April 1928, H. M. Pendlebury (BM, ML); Penang, 1 ♂ “Poulo-Pinang” (= Penang), leg. Drewsen (type, MHNG), 1 ♂ Batu Feringgi Catchment Area, 2 June 1960, H. T. Pagden (BM), 1 ♀ 1 ♂ Sungei Pinang, 1500 ft, 3 June 1962, ex nest of 15½ cells on *Marasmius*, H. T. Pagden (ML), 3 ♂ Batu Feringgi, 25 Febr. - 1 March 1963, M. A. Lieftinck (ML); Selangor, 1 ♂ Ampang Waterworks Reserve, 15 Aug. 1926, C. Dover (BM).

Singapore: 1 ♀ coll. Baker (USNM).

Sumatra: Nias Isl., 1 ♀ Lelemboli, Aug. 1886, leg. Modigliani (*cilipennis* det. Buysson) (MCG); Palembang, 4 ♂ Pagar Alam, 750 m, 23 May 1935, Mrs. M. E. Walsh (BM, 1 ♂ ML).

Belitung Isl.: “West Billiton”, Tjerutjuk, sea level, 1 ♂ 2 Aug. 1935, 1 ♀ 2 ♂ 14 Dec. 1936, F. J. Kuiper (ML).

Borneo: 1 ♂ “Borneo”, leg. F. Baczcs (NMW); Sarawak, 1 ♂ “Sarawak”, 1897, R. Shelford (BM); 8 ♂ Kuching, 1899-1900, Dayak collector, from R. Shelford (OUM, 2 ♂ ML), 1 ♀ River Kapah, trib. of R. Tinjan (MCZ).

Palawan: 2 ♂ Brooke's Pt., Tigoplan River, 500-700 ft, Philipp. Zool. Exp., F. G. Werner leg. (CNHM, ML).

Java: West Java, Bogor (“Buitenzorg”), Djasinga, 150 m, at river Tjibarangbang, 2 ♂ April 1935 and Nov. 1936, 2 ♀ Febr. and June 1937, M. A. Lieftinck (ML), 1 ♀ 2 ♂ July 1937, J. and E. van der Vecht (ML); 1 ♂ Wijnkoop Bay, Dec. 1936, Mrs. M. E. Walsh (ML), 1 ♂ Djampang Wetan, Radjamandala, 1200 ft, Nov. 1937, Mrs. M. E. Walsh (BM).

### **Female**

Very similar to *M. cilipennis*, but easily distinguished by the characters mentioned in the key on p. 64. Further differences are as follows.

Preocular part of clypeus slightly longer than one-fifth of length of head; interocular part in profile slightly less convex than in *M. cilipennis*; in centre of clypeus the interspaces between the punctures smooth and shining. Lateral areas

of mesoscutum (on outer side of prescutal furrows) superficially rugose and slightly less shining than in *M. cilipennis*.

Yellow markings rather constant, but the dark line on the clypeus frequently less narrowed at base than in Fig. 28.

#### Male

Apart from the colour characters mentioned in the key, distinguished by the mid tibia, which is less dilated (especially the basal half narrower), with outer side slightly convex and shiny and bearing a few outstanding hairs.

Yellow spot at apex of clypeus sometimes indistinct or absent; black supra-antennal mark may be smaller than in Fig. 31; pale stripe on dorsal side of antennae (Fig. 33) usually present on the terminal six segments, rarely also on segment 7 (in one ♂ from Java). Gastral tergite 1 with elongate dorsal spot on bulbus, 2 with lateral spot below spiracle, 3 brown or with small lateral spot, 4 and 5 with moderately wide yellow band in the middle of the tergite, separating an anterior translucent area (whitish in living insect?) from the dark posterior part, which is widened laterally, the yellow band often separated from a lateral spot of the same colour, 6 whitish with rather narrow dark posterior margin; sternites 2-5 mainly as in ♀, but some spots may be reduced or absent, 6 with irregular yellow band at base; terminal segment whitish, ventrally mainly yellow.

In the two males from Palawan only antennal segments 10-13 are mainly whitish dorsally, and the pale-coloured part of segment 9 covers less than its half. Since the mid tibiae of these males are somewhat duller than in the other specimens, examination of additional material from this island is desirable.

#### **Holischnogaster** gen. nov. (Fig. 38-49)

Head (Fig. 38 and 43), including clypeus, nearly as wide as high in ♀, slightly wider than high in ♂. Clypeus longer than wide, narrowed into a truncate point in ♀, in ♂ relatively shorter with nearly regularly triangular anterior portion. Mandibles rather long, tridentate, crossing when at rest. Malar space short in ♀, slightly longer in ♂. Mouthparts (Fig. 39 and 43) long, apical lobes of the narrow glossa (in preserved specimens) not divergent; segment 2 of maxillary palpi longer than other segments, but less than twice as long as any of these; segment 1 of labial palpi about as long as 2-4 together. Antennae clavate, gradually swollen from segment 6 to 10 (♀) or 11 (♂), and here more than twice as thick as at segment 6. Occipital carina meets hypostomal carina near base of proboscideal fossa. Vertex without impressed median line behind ocelli.

Thoracic complex (measured in lateral aspect) slightly longer than half the length of gastral petiole (4 : 7), general shape as in *Parischnogaster*, but in ♂ the sides without any trace of specialized pubescent areas. Mesoscutum without prescutal sutures.

Legs slender, not modified in ♂.

Wings mainly as in other Stenogastrinae, but the second submarginal cell only moderately wide and narrowed towards the radial cell, the first cross-vein (Rs) being rather strongly reclivous (front end farther from wing base than hind end).

Nervulus (cu-a) usually placed before the fork of M and Cu; vein Cu<sub>1</sub>b strongly reclivous. Hamuli (wing hooks) 6-8, as usual in this subfamily, widely and somewhat irregularly spaced. Anal lobe of hind wing very small.

Gastral petiole (Fig. 40 and 41) slender, bulbus elongate, its width slightly more than three times the smallest width of the cylindrical part. Spiracles of petiole and

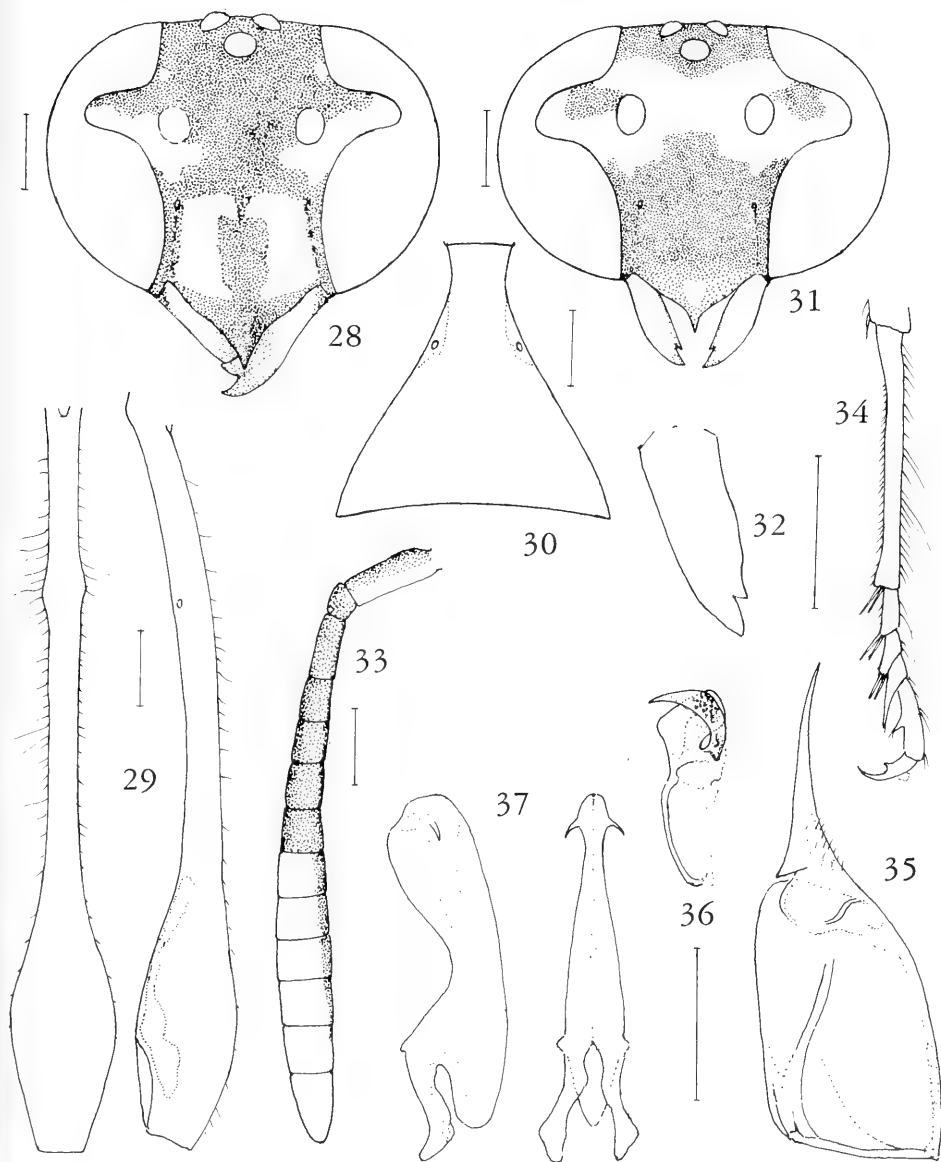


Fig. 28—30. *Metischnogaster drewseni* (Saussure) ♀, Penang. 28, head; 29, gastral petiole, dorsal and lateral views; 30, gastral segment 2, dorsal view. Fig. 31—37. *Metischnogaster drewseni* (Saussure) ♂, Java. 31, head; 32, mandible, lateral view; 33, antenna; 34, fore tarsus; 35, paramere; 36, volsella; 37, aedeagus, lateral and dorsal views. Scale lines represent 0.5 mm.

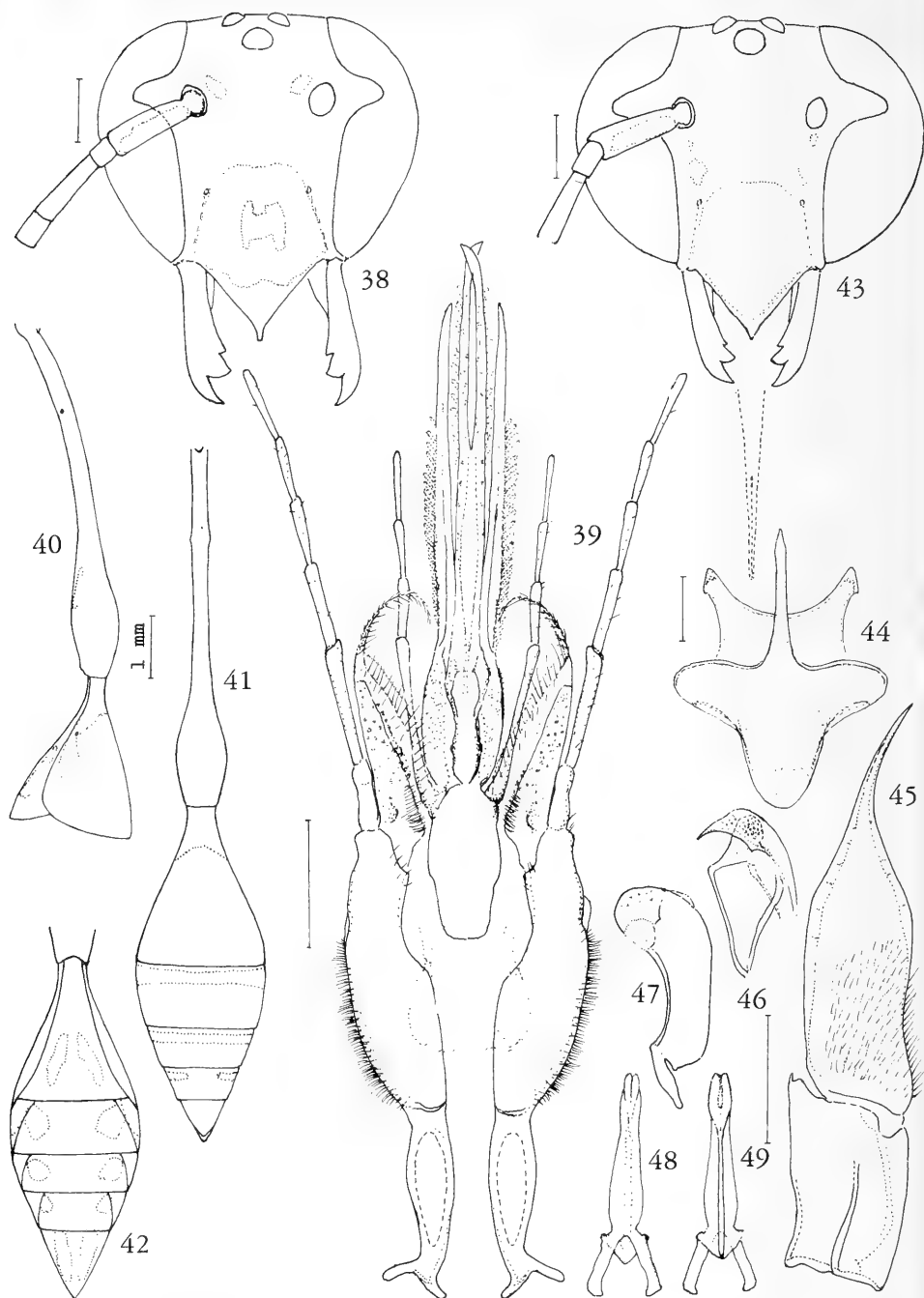


Fig. 38—42. *Holischnogaster gracilipes* sp. n. ♀, Borneo. 38, head; 39, mouthparts, ventral view; 40, gastral segments 1 and 2, lateral view; 41, gaster, dorsal view, segments 3—6 extended to show yellow markings; 42, segments 2—6, ventral view. Fig. 43—49. *Holischnogaster gracilipes* sp. n. ♂, Borneo. 43, head (length of glossa indicated by dotted lines); 44, gastral sternites 7—8, flattened; 45, paramere; 46, volsella; 47—49, aedeagus, lateral, ventral and dorsal views, respectively. Scale lines represent 0.5 mm (except Fig. 40 and 42).

segment 2 visible in ventral aspect, the latter distinctly placed before midlength of tergite. Segment 2 (Fig. 41) longer than wide at apex, slightly constricted at base. Male genitalia mainly as in *Parischnogaster mellyi* group, but aedeagus more strongly curved and higher.

Type species: *Holischnogaster gracilipes* spec. nov.

Distribution. — Borneo and Sumatra.

Note. — The type-species is closely related to *Parischnogaster*, as is evident from the structure of the male genitalia. I have provisionally treated it as a separate genus, because the lengthened mouthparts of both sexes and the non-dilated mid tarsi of the male suggest that there may be important differences in behaviour with regard to feeding and mating. Investigations on these points would be very valuable. Also discovery of the hitherto unknown nest construction might give important information on possible relationships.

***Holischnogaster gracilipes* spec. nov. (Fig. 38-49)**

Material. — Borneo: Sabah, 3 ♀ 5 ♂ Mt. Kinabalu, 5000 ft, 1-5 May 1973, K. M. Guichard (holotype ♀ and allotype ♂ in coll. Giordani Soika, paratypes: coll. Giordani Soika, 1 ♀ 2 ♂ ML); 1 ♂ Penrissen, May 1899, Shelford leg. (paratype, BM 1910-203); Sarawak, 1 ♀ Mt. Dulit, primary forest, 26 Oct. 1932, Oxford Univ. Exp., B. M. Hobby & A. W. Moore (BM 1933-254) (gaster lacking).

Sumatra: 1 ♂ Sungai Kumbang, Sept. 1915, Edw. Jacobson, no. 85-13 (antennae and gaster lacking) (ML).

**Female**

Clypeus faintly shining, punctate on microsculptured, reticulate-coriaceous ground; the punctures varying in size, small and close at the base, larger in centre and anteriorly and here separated by one or more puncture widths; apex of clypeus bluntly keeled. Supraclypeal area not distinctly separated from clypeus, dull and densely punctate, at level of lower margin of antennal sockets with short median keel (hardly more than elongate low tubercle). Frons and vertex dull, more rugosely punctate.

Pronotum dull, transversely rugose-striate, the striae coarsest in anterior-lateral angles. Mesoscutum and scutellum dull, densely rugose-punctate, the anteriorly dilated space between median scutal lines superficially roughened and more shining. Mesepisternum: upper part dull, irregularly obliquely striate, hypopimeral area slightly more shining and superficially rugose, transverse suture with row of punctures; ventral part swollen, rugosely punctate-striate, on each side with trace of precoxal suture. Metanotum finely rugose-punctate, metapleura moderately shining. Propodeum rather shining, finely obliquely striate, the striae sharply defined on dorsal surface, somewhat irregular and running into puncturation at lateral margins.

Gastral segments impunctate, with very fine and superficial microsculpture.

Face with short, appressed, golden pubescence and moderately long outstanding hairs; longer hairs are present at apex of clypeus and on mandibles. Pubescence of thorax and legs generally longer than in *Parischnogaster mellyi* (Saussure), gastral petiole with rather long outstanding hairs.

Ground colour dark brown to blackish; thorax, legs and abdomen partly pale brown; the following parts yellow: mandibles (brownish at margins and on teeth), clypeus (except for narrow band at anterior margin and irregularly shaped mark in centre), underside of antennal scape, spot on genae at mandible base, pronotal collar, band at posterior margin of pronotum, narrowly interrupted medially and strongly dilated at shoulders, two elongately triangular spots on anterior part of mesoscutum, broad band at base of scutellum and small spot on maxilla, large vertical spot on upper part of mesepisternum and an even larger one on lower part, bordering on the transverse suture, broad sublunate band on disk of metanotum and small triangular spot in anterior angle of lateral cavity, spot on metapleura beneath base of hind wing; propodeum except subquadrate area at base, produced on each side along anterior margin, and irregular band on lateral surfaces; greater part of coxae, lines on femora and tibiae I, II, and distal half of III, line on basitarsus of fore legs; markings on gaster as shown in Fig. 40-42.

Length (h. + th. + t. 1+2): 12-13 mm.

### Male

Very similar to female, mainly differing in shape of head and clypeus (Fig. 43); yellow markings generally somewhat more extensive, but evidently rather variable; clypeus entirely yellow, supraclypeal area with yellow spot on each side (sometimes reduced, as in Fig. 43, or absent), yellow spot on genae larger than in ♀, spots on mesoscutum longer, in some specimens produced backwards as an interrupted line which ends at level of posterior margin of tegulae; dark area at base of propodeum reduced, subtriangular; yellow line on tibiae III either entire or narrowly interrupted; gastral tergite 1 with narrow lateral line on basal half of bulbus, 2 as in ♀, 3 with broad yellow basal band (anteriorly with brownish area narrowed towards the sides), the brown posterior part of the tergite covering less than half the length in the middle and much less at the sides; 4-6 with broad yellowish-white basal band, leaving only a narrow dark band at posterior margin, 7 yellowish-white on basal half; sternites mainly as in ♀, terminal sternite with yellow spot, its narrowed posterior part brownish.

Length apparently not different from that of ♀.

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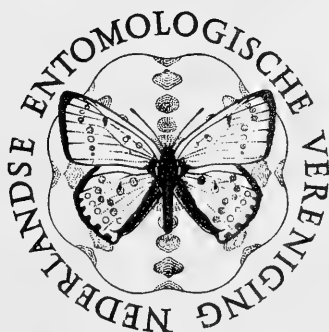
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## INHOUD

J. KRIKKEN. — Asian bolboceratine scarabs of the genus *Bolbogonium* Boucomont (Coleoptera: Geotrupidae), p. 77—108, text-figs. 1—30, frontis-piece, pls. 2—3.









Plate 1. *Bolbogonium insidiosum*, a new species from southern and central India (holotype male from Coimbatore, total length ca 8.5 mm).

# ASIAN BOLBOCERATINE SCARABS OF THE GENUS *BOLBOGONIUM* BOUCOMONT (COLEOPTERA: GEOTRUPIDAE)

by

J. KRIKKEN

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With 43 figures and one frontis-piece

## ABSTRACT

After a brief introduction to and technical remarks on this first paper in a series on the classification of Asian Bolboceratini, the genus *Bolbogonium* Boucomont is revised. *Bolbogonium* is here raised to generic rank, diagnosed, and the 10 known species are keyed, described and illustrated. The distribution of the genus is mainly Oriental. The three forms previously named are *Bolbogonium impressum* (Wiedemann) comb. nov., *punctatissimum* (Westwood) comb. nov., and *triangulum* (Westwood) comb. nov. (type-species). Of *impressum* and *triangulum* new records are given. The following new species are treated: *addendum* (Vietnam), *bicornutum* (India), *howdeni* (India, Pakistan), *insidiosum* (India), *pseudopunctatissimum* (India), *scurra* (India), and *wiebesi* (Burma).

A survey of characters and character states relevant to a supraspecific classification of the world Bolboceratini is given in an appendix.

## INTRODUCTION

This paper is the first in a series on the Asian representatives of the tribe Bolboceratini (sensu Howden & Martinez, 1963). Both this series and related work are intended to contribute to a world-wide reclassification of the group, particularly on the supraspecific level.

During the past few years I have tried to assemble as many Asian bolboceratines as possible, but the number of specimens so far received from many institutions and individuals remained highly disproportional to my efforts, particularly from the geographic point of view. This is, among other factors, certainly due to the retiring habits of bolboceratines and to regional undercollecting; vast areas, although in all probability inhabited by bolboceratines, do not seem to have produced a single specimen. Consequently, the taxonomy and distribution of these scarabs cannot be dealt with in a final or authoritative manner, and sooner or later supplementary results are to be expected.

Reliable data on the bionomics of the Asian species are not available, but undoubtedly in the day-time the animals hide in deeply excavated terrestrial burrows, as their European and North American relatives notoriously do (for a summary of the known life-histories, see Howden, 1955: 296—299); they might as well feed on and provide their brood burrows with subterranean fungi or other

vegetable matter. The label data indicate that several of the specimens before me were attracted to light; actually, the majority may have been collected in this way.

The only comprehensive study on Asian Bolboceratini ever published was written by Westwood (1852), who treated 22 species, omitting 7 names published by earlier workers. Consultation of Westwood's specimens proved indispensable, but, unfortunately, part of the original material could not be traced. Later workers added 15 new species-group names based on material from tropical and eastern Asia, bringing the total to 44, of which two have been synonymized. The species were accommodated in seven genus-group taxa, including one subgenus. The last complete genus-group classification was given by Boucomont (1911) in a treatise on the world fauna. He then proposed the subgenus *Bolbogonium* for *Bolboceras triangulum* Westwood. The taxonomy of this group, here raised to generic rank, is worked out below.

The publication of a modern classification of the Asian genus-group taxa is postponed, since this would entail the introduction of new names before the taxonomy on the species-group level has been established to a reasonable degree. A second reason for postponing is the fact that Howden and I are trying to work out the classification of the world fauna. Some of the Asian groups are closely related to or have members in the fauna of tropical Africa, and the taxonomic characters of these are still under investigation. Despite this omission, the generic diagnosis of *Bolbogonium* given hereafter warrants a correct recognition, as the features included implicitly match those of allied groups to be treated in forthcoming papers.

In an appendix I give an analysis of the characters relevant to a comprehensive classification of the world fauna, which may serve as a matrix for diagnoses of genus-group taxa. Sixty-six characters are listed; 23 unconditional and 8 conditional characters are suggested to be of primary importance in a supraspecific classification. This does not necessarily mean that they are constant in all groups. Although I have included classified character states derived from bolboceratines of all the zoogeographic regions, the present survey is undoubtedly capable of improvement and extension. The Australasian fauna seems incompletely surveyed, at least as far as cephalic and pronotal armature is concerned. The classification of the male genitalia is strongly simplified, mainly because of the lack of information on the homologies of their elements. Most statements are phrased in a generalized manner, and in actual cases need further specification. To give only one example, I have no pretention at all to present a complete survey of the excessive diversity in pronotal armature among Bolboceratini (characters 18 et seq.). Only a few of the characters listed can be used for phylogenetic research.

#### PRESENTATION OF DATA

The descriptive work was done with the aid of a Wild M5 binocular microscope (magnifications  $\times 6$ - $\times 100$ ) plus drawing apparatus. Most distances and densities were established by comparing the optical picture with verified scales viewed through the drawing apparatus. Cephalic distances and densities were established in full-face view, i.e. with the cephalic plane perpendicular to the optical axis.

Other measurements and counts, unless mentioned otherwise, were established after placing the specimen with the plane touching the scutellum perpendicular to the optical axis. The absolute values must be interpreted very carefully, since measurements on such convex scarabs like *Bolboceratini* are inherently inexact.

The information in my descriptions varies slightly according to genus, number and status of specimens available, and according to quantity and nature of information in previous publications. In the present revision of *Bolbogonium* detailed descriptions of all the species are given. As a rule little attention is paid to the pectoral and abdominal characters. The abdomens of many specimens had to be extracted in order to examine the genitalia. In *Bolbogonium* I suspect that at least one species exhibits sexual dimorphism in its clypeofrontal ornamentation (see below, section on the genus, infrageneric dissimilarities, character 2); in some other species, however, the sexes are definitely similar. I noticed that some workers had sexed their specimens incorrectly, this being due to the small size of the phallus in the groups concerned; in several instances the abdomen had been ruined completely, or it was simply missing.

Both the photographs of the general appearance and the drawings of the cephalic and pronotal contours serve to relieve the descriptions of some information difficult to communicate verbally. Unless mentioned otherwise, all the scale lines given with the figures represent 1 mm. Some of the quantitative data in the specimen descriptions have potential reference value only.

Clearly different size classes of sculptural elements (e.g. punctures) may be mixed on a particular surface. In the descriptions this is indicated as double (two size classes occur), triple (three size classes occur), etc., the elements being termed primary (the largest), secondary, tertiary, etc. for each particular surface.

In *Bolboceratini* the number of fossorial elevations on the outer side of middle and hind tibiae is difficult to establish. The height of these elevations decreases from apex to base, and usually proximally only a number of spines indicate their position. In the descriptions the number of indistinct proximal fossorial elevations (usually those lacking a continuous crest) is placed between parentheses.

Despite poor collection data, the localities of the species are mapped; the distribution of the genus (shaded, fig. 1) is hypothetical.

The following abbreviations concerning the location of *Bolbogonium* material are used:

- BH — Zoologisches Museum der Humboldt-Universität, Berlin;
- BM — British Museum (Natural History), London;
- CNC — Canadian National Collection, Ottawa;
- L — Rijksmuseum van Natuurlijke Historie, Leiden;
- P — Muséum National d'Histoire Naturelle, Paris;
- M — Zoologische Staatssammlung, Munich;
- SMT — Staatliches Museum für Tierkunde, Dresden.

### Genus *Bolbogonium* Boucomont stat. nov.

*Bolbogonium* Boucomont, 1911: 340 (as subgenus of *Bolboceras* Kirby; type-sp. *Bolboceras triangulum* Westw.), 342 (in key).

**Generic diagnosis.** — Middle coxae widely separated by anterior lobe of metasternal disc, which is pyriform (fig. 28). Glabrous shiny area on proximal side of club segment 1 large, and distinctly separated from surrounding pubescent surface (fig. 27). Seven striae between suture and humeral umbone, all virtually reaching base (fig. 26). Vertex laterally limited by arcuate crest, posterior margin more or less concavely acclivous. Pronotum anteriorly with either simple or more complex, characteristically shaped impression, usually surmounted by simple or bisinuate crest (i.e., at most with single median protrusion).

Outer margin of right mandible with distinct arcuate lobe. Labrum thickened, surface frequently heavily sculptured. Clypeal outline (dorsal view) variant: semicircular, semielliptic or trapeziform, with or without anterolateral or antero-median marginal protrusion(s). Perimarginal ridge of clypeus variably distinct. Clypeus at most with low median longitudinal elevation; clypeofrontal transition or frons with either single protrusion or set of protrusions, always situated discally. Head never with simple transverse ridge between eyes. Frontovertex with or without impression(s). Anterior border of eye-canthus marginate. Eyes entire, not

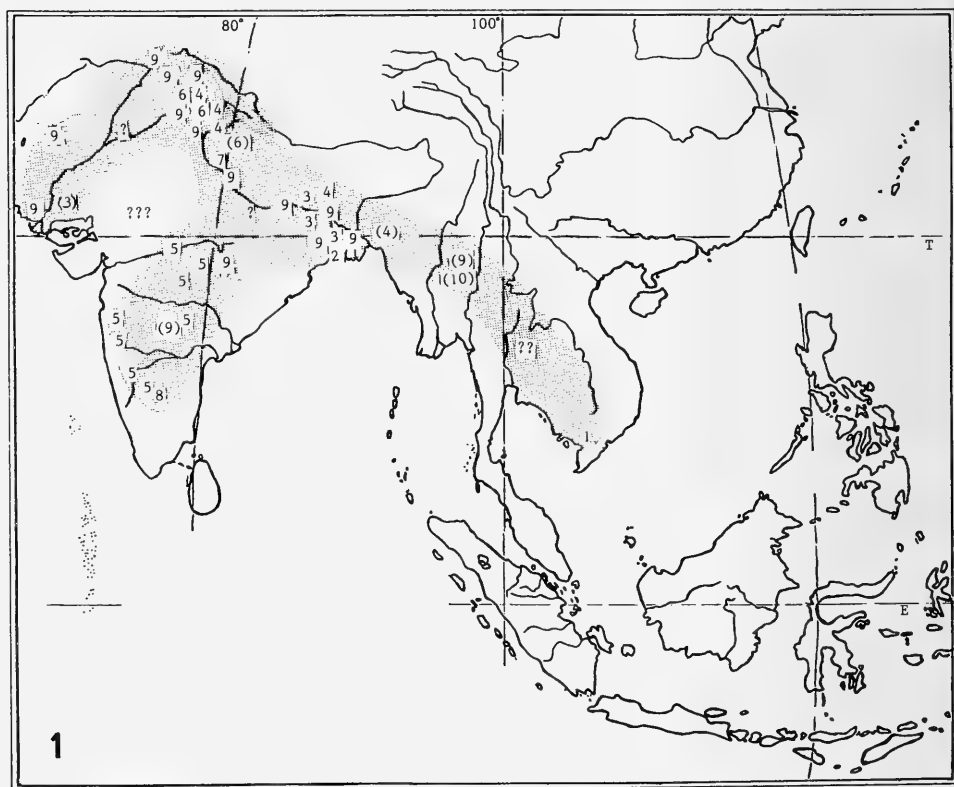


Fig. 1. Approximate known distribution of *Bolbogonium* (shaded) and its species. 1, *addendum*; 2, *bicornutum*; 3, *howdeni*; 4, *impressum*; 5, *insidiosum*; 6, *pseudopunctatissimum*; 7, *punctatissimum*; 8, *scurra*; 9, *triangulum*; 10, *wiebesi*. Numbers between parentheses refer to insufficiently detailed locality data (usually country or province records).

divided into two parts. Pronotal base marginate (at least medially). Scutellum virtually triangular, ratio  $l/w$  1—1.5. Elytral base unmodified; epipleuron reaching apicosutural angle. Elytral interstriae scarcely convex, striae at most weakly impressed. Antennal club unmodified; outline approximately ovate (ratio  $l/w$  of lamellae exceeding 1.5; fig. 27). Prosternum unmodified. Subapical fossorial elevations of middle and hind tibiae (fig. 29) with either angulate or arcuate crest; at least two complete non-apical fossorial elevations present. Metatarsus of middle and hind legs relatively short, length not exceeding maximum width of tibial apex. Parameres small, poorly sclerotized, simple (fig. 31). Body medium-sized, length roughly around one cm. Colour uniformly brown, orange, or yellow.

Type-species. — *Bolboceras triangulum* Westwood, by original designation.

Affinities. — *Bolbogonium* species superficially resemble *Bolboceras indicum* Westwood and its allies. They differ, however, greatly in characters of the antennal club, striation on the elytral base, shape of metasternum, etc. The primary set of properties, as mentioned in the first paragraph of the above diagnosis, warrants a generic status, and Boucomont's subgenus is here treated accordingly.

Infrageneric dissimilarities. — The following properties proved to be important in a classification of *Bolbogonium* (see comparative drawings):

- 1, shape of clypeus simply trapeziform (a), clypeus with produced anterolateral angles (b), or clypeus more or less produced anteromedially (c).
- 2, detailed structure of clypeofrontal ornamentation; frons with variably developed transverse ridge (a), with two small, isolated (paramedian) tubercles (b), with three small, isolated tubercles (c), with simple median tubercle (d), with a different ornamentation (e), — note that this may be a sexual character.
- 3, frontolateral ridge distinct (a), or (sub)obsolete (b).
- 4, vertex generally flat (a), or with distinct U-shaped impression (b).
- 5, anteromedian impression of pronotum absent or superficial (a), or anteromedian impression well pronounced (b).
- 6, conditional on 5 (b); pronotal impression with large, well-defined (sub)horizontal space immediately behind anterior border (a), or such a horizontal space absent (b).
- 7, bisinuate crest of pronotum absent or ill-defined (a); or pronotum with distinct crest, which is either moderately defined (b), or sharply defined (c).
- 8, basal margin of pronotum completely ridged (a), or incompletely ridged (usually medially only) (b).
- 9, non-apical fossorial elevations on middle and hind tibiae with either arcuate (a), or angulate (emarginate, bilobate) crest (b).
- 10, sculpture of dorsum — not classified.

The structure of the male genitalia is rather simple; they are generally poorly sclerotized, and consequently provide no characters of practical diagnostic value.

The distribution of the classified character states over the species recognized within *Bolbogonium* is given in the following table.

On these characters four species-groups may be recognized within *Bolbogonium*, viz. the *bicornutum* group (with *addendum* and *bicornutum*), the *triangulum* group (with *pseudopunctatissimum*, *triangulum* and *impressum*), the *insidiosum* group (with

Character no.	1	2	3	4	5	6	7	8	9
<i>addendum</i>	a	a	b	a	a	(b)	a	b	a
<i>bicornutum</i>	a	a	b	a	a	(b)	ab	b	a
<i>pseudopunctatissimum</i>	b	a	a	a	a	a	a	b	a
<i>triangulum</i>	b	b/e	a	a	b	a	a-b	a	a
<i>impressum</i>	b	d	a	a	b	a	b	a	a
<i>scurra</i>	a	e	ab	a	b	b	b	b	a
<i>insidiosum</i>	c	e	a	b	b	b	b	b	a
<i>punctatissimum</i>	c	b	b	a	b	b	b	a	b
<i>howdeni</i>	c	c	b	a	b	b	b	a	b
<i>wiebesi</i>	c	d	b	a	b	b	c	a	b

*insidiosum* and *scurra*), and the *punctatissimum* group (with *punctatissimum*, *howdeni* and *wiebesi*).

There is no basis to discuss the phylogeny of *Bolbogonium*, since the significance of most characters is unknown.

Distribution. — Oriental, transgression into Palearctic (fig. 1): 10 species recorded from localities ranging from Pakistan to South Vietnam, no material seen from North of the Himalaya.

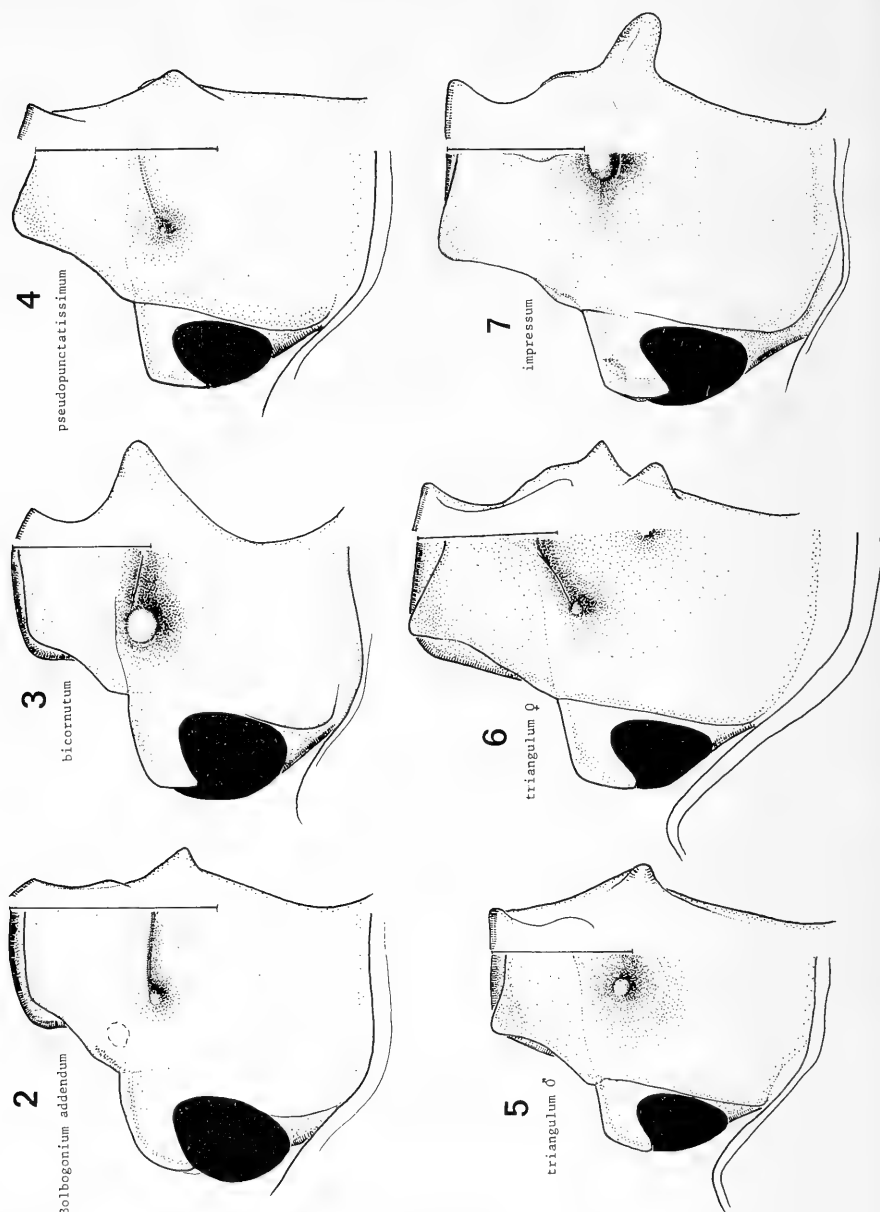
Bionomics. — Apparently nocturnally active; found "in soil"; record from dung considered casual.

#### Key to the species of *Bolbogonium* (see figs. 2—25)

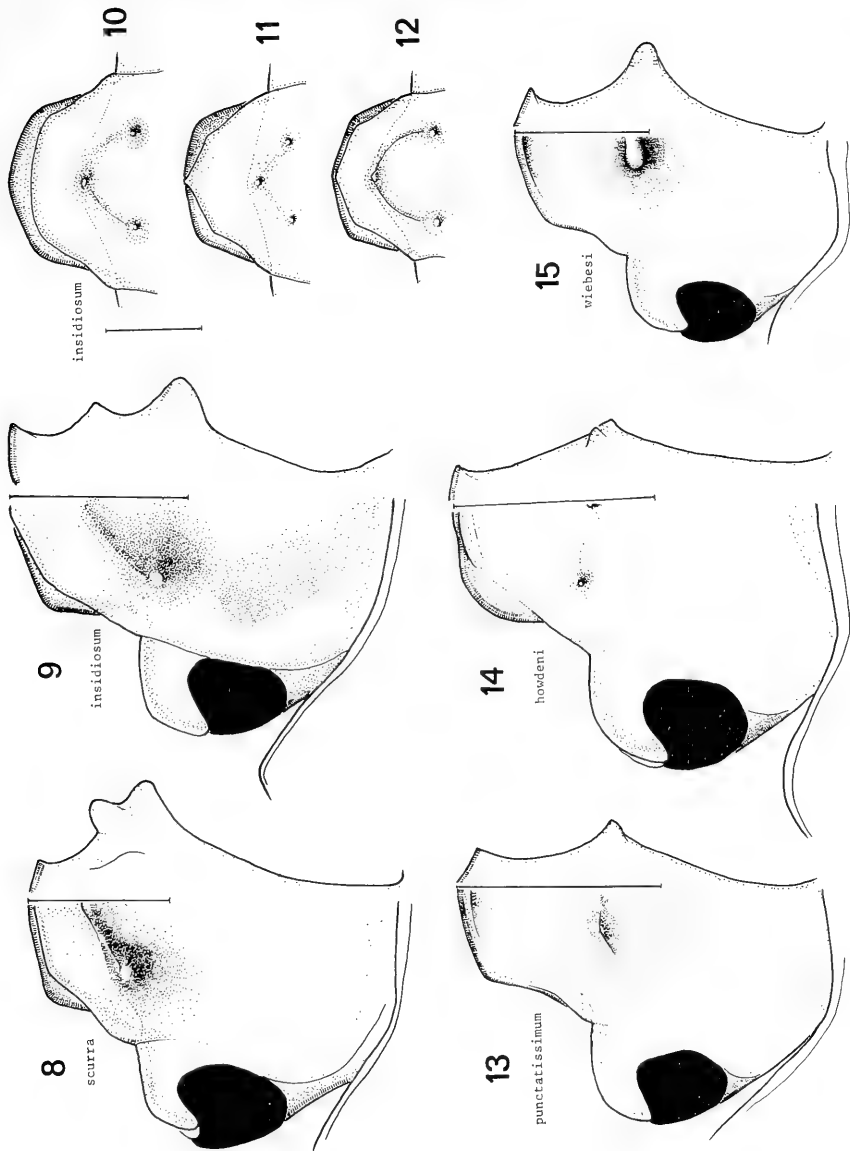
1. Anterolateral angles of clypeus distinctly raised, produced. Impression of anterior side of pronotum with (sub)horizontal base. Vertex lacking symmetrical impression(s). If there are only two frontal tubercles, these are not connected by a conspicuous saddle. Subapical fossorial elevations of middle and hind tibiae with arcuate crest. Pronotal base completely marginate (except in *pseudopunctatissimum*). Frontolateral ridge usually distinct. Eye-canthus with more or less distinct anterolateral angle . . . . . 2
- Anterior border of clypeus either approximately straight with simply obtuse anterolateral angles, or rounded with obsolete anterolateral angles. Impression of anterior side of pronotum lacking well-defined horizontal base . . . . . 5
2. Frons with well-pronounced median tubercle between eyes, and a longitudinal callosity on clypeus. Pronotal crest distinct, and shifted to posterior half of pronotum. Length 9.5—13 mm. — N. India . . . . . *impressum* (p. 92)
- Frons with set of two or three elevations . . . . . 3
3. Frons between eye-canthi with pair of low tubercles separated by about half the intergenal distance, connected by arcuate ridge. Pronotal crest ill defined, and shifted to posterior half of pronotum. Length 7.5—11 mm. — N. India . . . . . *pseudopunctatissimum* (p. 90)
- Frons with different set of elevations, or with pair of approximated tubercles . . . . . 4



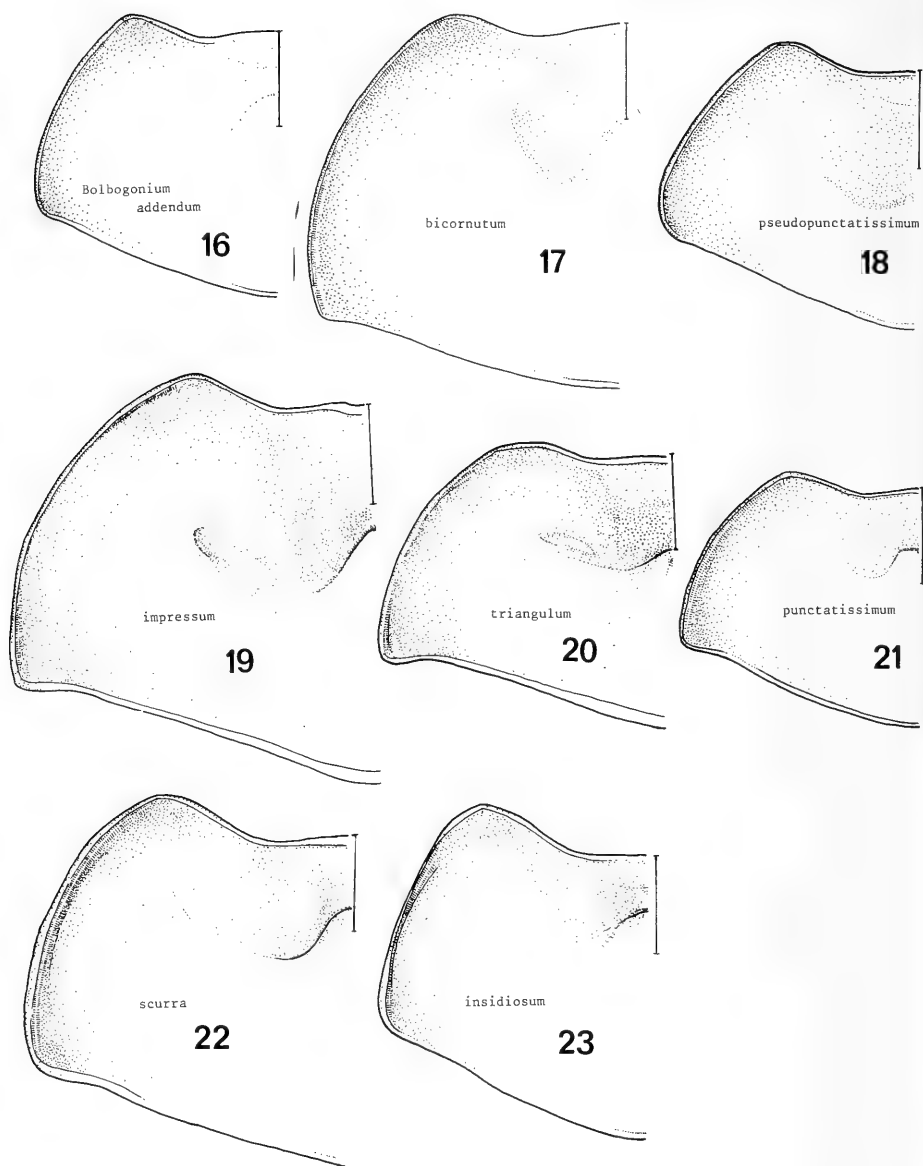
4. Frons with pair of approximated tubercles. Length 7.5—10 mm. — Burma, India, Pakistan . . . . . *triangulum* ♂ (p. 91)
- Frons with transverse ridge directly behind clypeofrontal suture, plus small central tubercle. Length 7.5—12 mm. — Burma, India, Pakistan . . . . . *triangulum* ♀ (p. 91)
5. Frons with pair of tubercles connected by variably developed rectilinear elevation. Anterolateral angles of clypeus distinct. Pronotal base medially feebly marginate. Frontolateral ridge indistinct . . . . . 6
- Frons with 1—3 tubercles, either isolated or connected by more or less pronounced V- or U-shaped elevation. Anterolateral angles of perimarginal ridge of clypeus (sub)obsolete, and clypeal margin usually either rounded, or with some anteromedian protrusion. If anterolateral angles distinct, frons with V-shaped elevation. Elytral striae distinctly impressed . . . . . 7
6. Frons with pair of widely separated small tubercles connected by vague ridge. Pronotum slightly impressed behind anteromedian border. Posterior declivity of vertex low. Length 8 mm. — S. Vietnam . . . . . *addendum* (p. 87)
- Frons with pair of widely separated stout tubercles connected by saddle. Anterior declivity of pronotum with characteristic impression. Length 11.5 mm. — NE. India . . . . . *bicornutum* (p. 89)
7. Frons with single transverse tubercle between eye-canths. W-shaped crest of pronotum sharply defined. Clypeus with transverse antero-marginal costa. Vertex lacking pronounced impression. Subapical fossorial elevations of middle and hind tibiae with arcuate crest. Length 10 mm. — Burma . . . . . *wiebesi* (p. 99)
- Frons with two or three tubercles, free or connected by ridge . . . . . 8
8. General elevation of clypeofrons with one anterior protrusion and a pair of posterior tubercles; anterior protrusion frequently obsolescent, occasionally only leaving its costiform connection between the posterior paramedian tubercles; clypeofrontal suture (as far as visible) medially slightly shifted forward. Pronotal base medially feebly marginate. Frontolateral ridge usually distinct. Subapical fossorial elevations on middle and hind tibiae with arcuate crest. Vertex sparsely punctate . . . . . 9
- Frons with two or three small, isolated tubercles between eye-canths. Pronotal base completely marginate. Frontolateral ridge indistinct. Distal fossorial elevations of middle and hind tibiae angulate-emarginate or bilobate. Vertex densely punctate . . . . . 10
9. Surface of vertex plane or nearly so. Elytral striae coarsely punctate, punctures sharply defined, stria 2 obsolete slightly past scutellar apex. Clypeus trapeziform, apex non-protuberant, slightly curved. Frontal elevation a wide-legged V. Length 8.5—11 mm. — C. India . . . . . *scurra* (p. 94)
- Surface of vertex symmetrically impressed, sparsely punctate. Elytral striae moderately punctate, stria 2 extending further caudad. Clypeus with rounded, more or less obsolete anterolateral angles, apex frequently protuberant. Frontal elevation usually U-shaped, never a wide-legged V. Length 7—11 mm. — S. and C. India . . . . . *insidiosum* (p. 95)



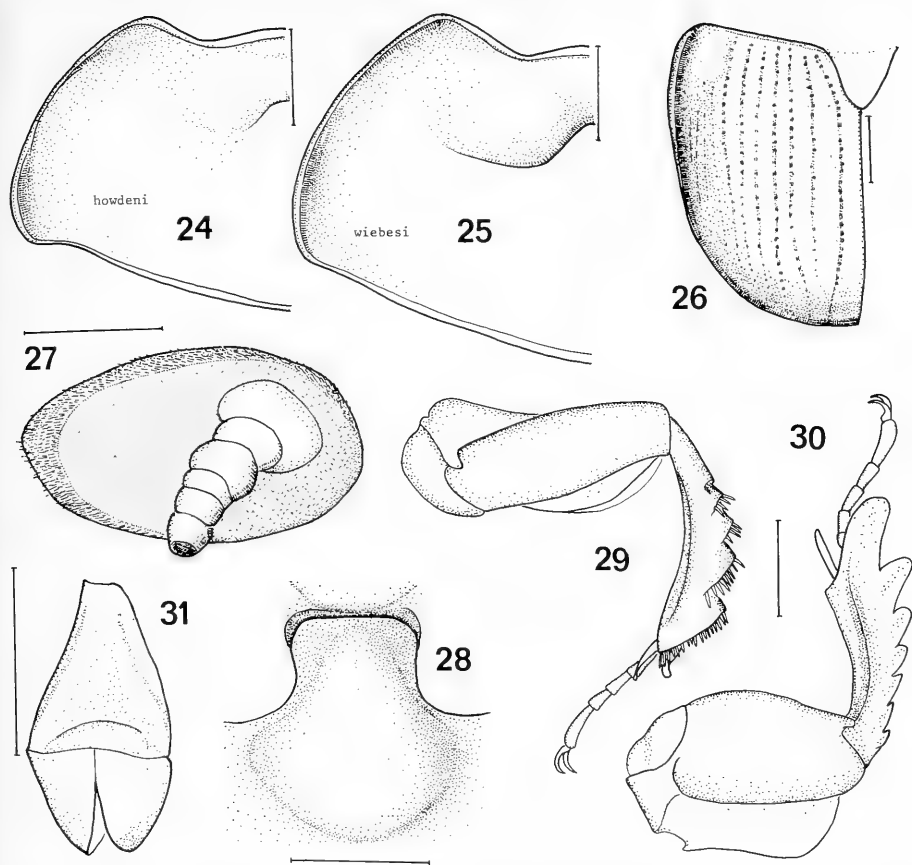
Figs. 2—7. Contours of left half of head (dorsal), with approximate left side profile. 2, *Bolbogonium addendum*, holotype; 3, *bicornutum*, holotype; 4, *pseudopunctatissimum*, holotype; 5, *triangulum*, ♂ Bengal; 6, ditto, ♀ Karachi; 7, *impressum*, ♂ Bengal.



Figs. 8—15. Contours of left half of head (dorsal), with approximate left side profile. 8, *Bolbogonium scurra*, holotype; 9, *insidiosum*, holotype; added figs. 10—12, polymorphism in shape of clypeofrons: Nagpur (10), Hoshangabad (11), and Coimbatore (12); 13, *punctatissimum*, holotype; 14, *howdeni*, holotype; 15, *wiebesi*, holotype.



Figs. 16—23. Contours of left half of pronotum (dorsal). 16, *Bolbogonium addendum*, holotype; 17, *bicornutum*, holotype; 18, *pseudopunctatissimum*, holotype; 19, *impressum*, ♂ Bengal; 20, *triangulum*, ♂ Bengal; 21, *punctatissimum*, holotype; 22, *scurra*, holotype; 23, *insidiosum*, holotype.



Figs. 24—25. Contours of left half of pronotum (dorsal). 24, *Bolbogonium howdeni*, holotype; 25, *wiebesi*, holotype. Figs. 26—31. Details of *B. triangulum* (26, 28—30, ♂ Haldwani; 27, ♀ Bengal; 31, ♂ Bengal). 26, left elytron, and scutellum; 27, flagellar segments and inward surface of first club segment; 28, metasternal plate; 29, left hind leg; 30, left fore leg; 31, phallus, dorsal. Scale line with fig. 27=0.5 mm, others 1 mm.

10. Frons with three small transversely collinear tubercles between eye-canths. Head and pronotum crowdedly punctate or punctate-rugulate throughout. Elytral derm moderately coarsely wrinkled, notably on lateral declivity. Length 9-11 mm. — N. India, S. Pakistan . . . . . *howdeni* (p. 97)
- Frons with pair of small tubercles between eye-canths. Pronotum densely or crowdedly punctate. Lateral declivity of elytron not conspicuously wrinkled. Length 8 mm. — N. India . . . . . *punctatissimum* (p. 96)

***Bolbogonium addendum* sp. nov. (figs. 2, 16, 32)**

Description (holotype, female). — Approximate length 8, width 5, height 4 mm. Orange-brown, shiny; tips, ridges, margins, sutures more or less infuscated; pilosity yellowish. Habitus, fig. 32.

Labrum short, almost rectilinear in front, sides rounded; surface rugulate. Cephalic contours, fig. 2. Clypeus flat, marginal ridges distinct; surface punctate-rugulate; clypeofrontal suture only laterally noticeable. Frons with pair of small, widely separated tubercles connected by feeble, virtually rectilinear ridge; general surface scarcely raised, between the eye-canths irregularly crowdedly punctate, almost punctate-rugulate; to the vertex this sculpture passes into double punctation; primary punctures approximately isodiametric, rather coarse, well-defined, closely and irregularly set, their diameters ca. 0.1 mm; secondary punctures distinct, their diameters roughly one-fifth of those of the primaries, mostly separated by at least their own diameter; frontolateral ridge indistinct. Eye-canthus with raised anterior margin, sculpture punctate-rugulate. Maximum length of head (exclusive of labrum) 1.95, maximum width 2.70 mm; ratio l/w 0.73.

Pronotal contours, fig. 16; surface of pronotum evenly convex, only surface immediately behind the anteromedian border depressed; anterolateral angles obtuse, posterolateral angles obsolete, widely rounded; pronotal base medially marginate. Pronotal punctation double; primary punctures approximately isodiametric, rather coarse, well defined and distinctly impressed, irregularly distributed, closely set, except on paramedian parts of disc; densities on sublateral surface ca. 30/sq. mm, their diameters ca. 0.1 mm; secondary punctures numerous, distinct, evenly distributed. Median length of pronotum 2.8, maximum width 4.7 mm; ratio l/w 0.60. Scutellum deltoid, with arcuate apex; surface virtually impunctate.

Juxtasutural punctures of elytron small, indistinct. Discal striae of elytron weakly impressed, striae on lateral declivity not impressed; punctures in striae approximately isodiametric, distinct, densely arranged, separated by a few times their diameters, which are ca. 0.05 mm; depressed peripunctural surface affecting interstriae. Discal interstriae hardly convex, with numerous minute punctures.

Fore tibia with 7 external denticles, their size decreasing proximad; terminal spur well developed, reaching approximately halfway tarsal segment 2. Femora all moderately setose beneath, without notable details. Middle and hind tibiae with spinose fossorial elevations increasingly developed distad; number on outer side of right middle tibia 3 + (2), on right hind tibia also 3 + (2); crests of non-apical elevations arcuate, apical one of middle tibia slightly emarginate; number of fossorial spines along crest of anteapical elevation on right hind tibia ca. 17, intermediate ones smaller than outer ones; spur of hind tibia scarcely tapering, nearly reaching tarsal segment 3.

Identification. — *Bolbogonium addendum* makes a comparatively pauperized impression, and one wonders whether this has to do with marginal geographic distribution or with mere individual variation. As with *B. bicornutum*, the dorsal outline of the clypeus is trapeziform; the frontal elevation is diminutive compared to *bicornutum*. The posterior declivity of the vertex and the anterior impression of the pronotum are ill pronounced.

Material examined. — Holotype only (P), which has the following label data: „Museum Paris/Cochinchine/Mont de Chaudoc/Harmand 1877”, „518/77”, „Museum Paris/Hte-Vera Paz/Bocourt 188—66”, „groupe de/Bolboceras triangulum West./ Asie!// Bolboceras (Amechanus”. Paulian (1945: 41) already mentioned this

specimen. It undoubtedly belongs in *Bolbogonium*, and I think that the first-mentioned label is the correct one.

***Bolbogonium bicornutum* sp. nov.** (figs. 3, 17, 33)

Description (holotype, female). — Approximate length 11.5, width 6.5, height 5.5 mm. Orange-brown, shiny; tips, ridges, margins, sutures more or less infuscated; pilosity yellowish. Habitus, fig. 33.

Labrum short, slightly emarginate in front, sides widely rounded, surface rugulate. Cephalic contours, fig. 3. Clypeal margins raised; surface crowdedly punctate to malleate-punctate; clypeofrontal suture distinct laterally. Frons with pair of stout subconical tubercles between eye-canths; tubercles connected by transverse saddle steeply descending to clypeofrontal transition, posterior surface gently sloping down to vertex; frons and vertex with distinct scattered, medium-sized, isodiametric punctures; punctures crowded just below black tubercular tips, elsewhere separated by a few times their diameters, which are ca. 0.05 mm; density medially ca 10/0.25 sq. mm; between these punctures several smaller, ill-defined, shallow punctures are noticeable; frontolateral ridge indistinct. Eye-canths with raised margin, surface punctate-rugulate. Maximum length of head (exclusive of labrum) 2.55, maximum width 3.55 mm; ratio 1/w 0.72.

Pronotal contours, fig. 17; anterior declivity characteristically, shallowly impressed; impression topped by gently declivous bisinuate crest, its median prominence not sharply projecting cephalad, discal midline shallowly depressed; anterolateral angles obtuse, posterolateral angles obsolete, widely rounded; pronotal base medially marginate, laterally lined with punctures. Pronotal punctation double; anterior impression, discal depression and lateral declivities with numerous scattered, approximately isodiametric, well-defined, infuscated punctures, mostly separated by at least one time their diameters, which are ca. 0.08 mm.; densities halfway lateral declivity ca. 20/sq. mm.; secondary punctures sparse, moderately evenly distributed, their diameters diminutive compared to primary ones. Median length of pronotum 3.9, maximum width 6.5 mm; ratio 1/w 0.59. Scutellum deltoid with slightly sinuate sides; surface with numerous small scattered, distinct punctures, closely set in front, elsewhere sparse.

Elytron with only stria 1 shallowly impressed, others are merely series of punctures; juxtasutural series of punctures well-developed. Strial punctures large, resembling those of pronotum, regularly spaced, diameters on disc ca. 0.08 mm., mostly separated by two or three times their diameters. Interstriae 2 etc. not noticeably convex, their surface with minute, indistinct, sparse punctures.

Fore tibia with 7 or 8 external denticles, their size decreasing proximad; terminal spur of both fore tibiae missing. Femora all moderately densely setose beneath, without notable details. Middle and hind tibiae with spinose fossorial elevations increasingly developed distad; number in right middle tibia 3 + (3), in right hind tibia 4 + (2); crest of non-apical elevations arcuate, apical crest of middle tibia angulate; number of fossorial spines along crest of anteapical elevation in right middle tibia 13; spines approximately equal-sized; only one slightly bent, acuminate spur and two tarsal segments present in right middle tibia, other accessories of middle and hind tibiae missing.

Identification. — *Bolbogonium bicornutum* is easily recognizable by the shape of the head, the dorsal outline of the clypeus being perfectly trapeziform, the frons bearing a remarkably high transverse elevation. Furthermore, the outline of the punctate impression on the anterior declivity of the pronotum is very characteristic. The elytral striation is most superficial, while the strial punctures are rather coarse, sharply defined.

Material examined. — Holotype only (M), from India: Calcutta.

***Bolbogonium pseudopunctatissimum* sp. nov. (figs. 4, 18, 34)**

Description (holotype, male). — Approximate length 7.5, width 5, height 4 mm. Brown, shiny; tips, ridges, margins, sutures more or less infuscated; pilosity yellowish. Habitus, fig. 34.

Labrum emarginate in front, sides widely rounded, surface rugulate-punctate. Cephalic contours fig. 4. Clypeus with raised anterolateral angles; surface rugulate-punctate; marginal ridge distinct; clypeofrontal suture distinct. Frons with pair of tubercles connected by low arcuate ridges; punctation of frontovertex double ( $\times 25$ ), contiguous in front, less dense on disc, where densities of primary punctures are 13-17/0.1 sq.mm, diameters ca. 0.08 mm; punctures well defined, distinctly impressed, isodiametric; frontolateral ridge distinct. Eye-canthus with weakly raised anterior margin, surface contiguously punctate. Maximum length of head (exclusive of labrum) 1.90, maximum width 2.40 mm; ratio  $l/w$  0.79.

Pronotal contours, fig. 18; anterior declivity only with subhorizontal base, lacking impression; transverse discal crest subobsolete, discal midline shallowly impressed; base medially marginate. Pronotal punctation double, laterally triple ( $\times 50$ ); primary punctures sparse on paramedian discal surface; secondary punctures large, isodiametric, distinctly impressed, tertiary punctures well defined, isodiametric, equal-sized; densities of primary punctures sublaterally 8-12/0.25 sq. mm, diameters of primary, secondary and tertiary punctures 0.15, 0.08 and 0.01 mm respectively. Median length of pronotum 2.5, maximum width 4.6 mm; ratio  $l/w$  0.54. Scutellum deltoid, moderately punctate.

Juxtasutural stria of elytron present; discal striae of elytron shallowly impressed. Strial punctures distinctly impressed, well defined, isodiametric, their diameters ca. 0.05 mm, separated by 1-2 times their own diameter; peripunctural impressions affect interstrial surface. Interstria 1 distinctly convex, other discal interstriae very weakly convex; punctation sparse, secondary punctures just visible at magnification  $\times 50$ .

Fore tibia with 7 external denticles, their size decreasing proximad; terminal spur well developed, reaching to apex of tarsal segment 2. Femora all moderately densely setose beneath, without notable details. Middle and hind tibiae with spinose fossorial elevations increasingly developed distad; number in right middle tibia 3 + (2), in right hind tibia 3 + (2); crest of non-apical elevations arcuate, apical elevation of middle tibia emarginate; number of fossorial spines along crest of anteapical elevation on right middle tibia ca. 10, all nearly equal-sized; spurs of hind tibia slightly tapering but with rounded apex, reaching to apex of tarsal segment 2.



Variation. — Length 7.5-11 mm. Holotype with obsolescent pronotal crest, which is slightly better defined in the paratypes.

Identification. — Because of its bituberculate frons, this species was confounded with *Bolbogonium punctatissimum*. It differs from that species by its produced clypeal angles, the ridge connecting the frontal tubercles, the poorly pronounced pronotal crest and the arcuate fossorial elevations on middle and hind tibiae. The frontal and pronotal characters mentioned also separate *pseudopunctatissimum* from its closest relative, *triangulum*. Contrary to the other species in the *triangulum* group, the pronotal base of *pseudopunctatissimum* is incompletely marginate.

Material examined. — 3 specimens.

Holotype with label reading „Musoorie/Mackenzie coll./10.vii-20.x.22” (BM). Paratypes, 1 ♂ from Himalaya (BM), and 1 ♂ from Himachal Pradesh: Simla, viii-1898 (SMT).

***Bolbogonium triangulum* (Westwood) comb. nov.**

(figs. 5, 6, 20, 26-31, 35-37)

*Bolboceras triangulum* Westwood, 1852: 26 (type-loc. Mussoree), pl. 4 figs. 20, 20a.

*Bolboceras (Bolbogonium) triangulum*; Boucomont, 1911: 340 (type-sp. of the subgenus); Boucomont, 1912: 14 (in catalogue).

Notes. — There are two groups of specimens here placed under *triangulum*, which at first sight differ by their frontal ornamentation (figs. 5, 6). One group, agreeing with the type, proved to consist of females; the other proved to consist of males; sometimes both forms were found in the same series. As no other morphological differences could be found, I consider the frontal ornamentation in this species a sexual character, despite the fact that such dimorphism was not found in other species. Furthermore, there is some variation in the arrangement of the frontal protrusions (compare figs. 35 and 36). More material is needed to confirm the present interpretation of *B. triangulum*.

Description. — Approximate length ♂, 7.5-10, ♀, 7.5-12 mm. Brown, orange or yellow; shiny; pilosity yellowish. Habitus, figs. 35-37.

Labrum short, emarginate in front, sides widely rounded, surface rugulate-punctate. Cephalic contours, figs. 5 (♂), 6 (♀). Clypeal surface rugulate-punctate; anterolateral angles of clypeus produced; clypeofrontal suture distinct. Frons with pair of approximated tubercles (♂), or with transverse, at the ends tuberculate ridge plus median interocular tubercle (♀); frequently with elongate callosity on clypeofrontal transition; frontolateral ridge distinct, extending to acute crest limiting vertex; anterior surface of frons rugulate-punctate; posterior surface punctate, punctures usually more abundant in ♂. Eye-canthus rugulate-punctate, with raised anterior margin.

Pronotal contours, fig. 20; anterior declivity with well-defined horizontal base, topped by distinct W-shaped crest plus lateral cavity; midline distinctly impressed, well defined behind median protrusion; pronotal borders entirely marginate. Pronotal punctation triple; secondary punctures very distinct, their diameters ca. one-fifth of the primaries; tertiary punctation scarcely distinct ( $\times 50$ ); primary punctation dense along discal midline, very dense or crowded laterally, punctures

deep, well defined; anterior declivity microreticulate, opaque. Scutellum (fig. 26) deltoid, densely, distinctly punctate.

Elytral contours, fig. 26; juxtasutural punctures fine. Elytral striae discally weakly impressed; punctures moderately defined, separated by 1-3 (or 4) times their diameters. Interstriae weakly convex, with very fine punctures, separated by several times their diameters.

Fore tibia (fig. 30) with 7 external denticles, their size decreasing proximad; terminal spur reaching to tarsal segment 2. Femora all moderately setose beneath, without notable details. Middle and hind tibiae (fig. 29) with spinose fossorial elevations increasingly developed distad, two or three non-apical elevations having a complete arcuate crest with ca. 15 approximately equal spines; terminal spurs well developed, approximately as long as tarsal segments 1 + 2.

Identification. — *Bolbogonium triangulum* females are immediately recognizable by their characteristic frontal ornamentation. Males (as interpreted here, see above) may be confounded with other species with a bituberculate frons. Within the *triangulum* group with its produced anterolateral clypeal angles, only *pseudopunctatissimum* has two frontal tubercles, but these are less approximated than in *triangulum*, and they are connected by a transverse ridge. In *triangulum* the pronotal crest is nearly always more strongly pronounced than in *pseudopunctatissimum*. The secondary punctures on the pronotum of *triangulum* are much larger in proportion to the primaries than in *pseudopunctatissimum*.

Material examined. — 36 specimens.

Holotype from India with label „Ind. or./Mussoore/in cow dung” (BM). I doubt if this ecological remark indicates a regular habit. Further specimens as follows (if sex is indicated this was established by extraction of genitalia).

India: Bengal, no further details (2 ♂, SMT, one labelled by Boucomont as *B. punctatissimum*); Bara Taunda [?], x. 1927, Konietzko (1, BH); Buxar (2 ♂, 1 ♀, SMT); Cawnpore [Kanpur], 12.i.1921, Vernon (1, BM); Chapra, Mackenzie (2 ♀, BM); Deccan (1, P); Dehra Dun, 13.vii.1928 (1 ♂, BM); Dhara, v.1943 (1 ♀, Forest Research Inst. and Colleges, Dehra Dun); Calcutta (1, M); Haldwani: Chakata Range, 23.vi.1930, Chatterjee (1 ♂, L); Kumaon (1 ♀, BM); Motinala R., 25.vi.1927, Chatterjee (1 ♀, BM); Naldera, 29.vi.1938, Beeson, in soil (1 ♀, Forest Research Inst. and Colleges, Dehra Dun); Pusa, 5.xii.1904, Watson (1 ♀, BM), 17.vii.1915, at light (1 ♀, BM), 1.i.1916, Bahadur, at light (1 ♀, BM), 2.iii.1920, Austin (1 ♀, BM), Pusa without further data (1 ♀, BM); Simla (1 ♀, BM). North India, no details (1 ♂, BM). — Burma, (1 ♂, seen by Boucomont, 1 ♀ with perfectly straight frontal ridge, BM). — Pakistan: Karachi, Bell (3 ♂, 1 ♀, 1, BM); Murree (1 ♂, seen by Boucomont, BM); Quetta, vii.viii.1933, Samuel (1 ♀, BM), vii.1936, Nazeer, peach plot, light trap (1 ♀, BM; frontal elevations poorly pronounced); Tarnab, 24.v.1916, Fletcher (1 ♂, BM; fig. 35).

### ***Bolbogonium impressum* (Wiedemann) comb. nov. (figs. 7, 19, 38)**

*Scarabaeus impressus* Wiedemann, 1823: 6 (type-loc. Bengal).

*Bolboceras impressum*; Boucomont, 1902: 5 (in catalogue); 1912: 10 (in catalogue).

Description. — Approximate length 9.5-13 mm. Brown, largely shiny; pilosity yellowish. Habitus, fig. 38.

Labrum short, slightly emarginate in front, sides widely rounded, surface rugulate. Cephalic contours, fig. 7. Clypeus shallowly concave behind strongly produced anterolateral angles; midline with elongate callosity interrupting distinct, virtually rectilinear clypeofrontal suture; clypeal surface entirely malleate-rugulate. Frons raised between eye-canths, medially with stout tubercle, the apex of which may be slightly bifid; surface malleate-rugulate, posteriorly normally punctate; frontolateral ridge distinct. Vertex shallowly depressed, arcuate lateral margins distinctly raised; punctation of vertex double; primary punctures scattered, approximately isodiametric, shallow but distinct, laterally closely set, medially mostly separated by a few times their diameters; secondary punctures minute, scarcely discernable ( $\times 50$ ), but numerous, evenly distributed. Anterolateral angle of eye-canthus raised, sculpture like that of clypeus and frons.

Pronotal contours, fig. 19; anterior side with conspicuous, more or less opaque impression; declivity topped by virtually W-shaped crest with distinct median protrusion; base of declivity virtually horizontal, its posterior limit nearly paralleling superior crest; surface in front of lateral part of superior crest with rugulate-punctate cavity; pronotal borders entirely marginate. Pronotal punctation triple; primary punctation sparse beside impressed discal midline, close to crowded laterally, anteriorly, and on discal midline; punctures distinct, mostly isodiametric, laterally more or less irregular; secondary punctures very small, their diameters about one-tenth of the primaries, evenly distributed discally; tertiaries scarcely noticeable ( $\times 50$ ). Scutellum deltoid; closely punctate, secondary punctures minute, numerous, evenly distributed.

Juxtasutural punctures of elytron fine. Discal striae of pronotum shallowly impressed; punctures infuscated, small, separated by 2-4 times their diameters. Interstriae very weakly convex, punctation double; primary punctures sparse, scattered, small, approximately isodiametric, separated by several times their diameters; secondary punctures minute, numerous, evenly distributed.

Fore tibia with 8 external denticles, their size decreasing proximad; terminal spur reaching to tarsal segment 2. Femora all moderately setose beneath, without notable details. Middle and hind tibiae with spinose fossorial elevations increasingly developed distad, two or three non-apical ones having a complete, arcuate crest; antepical crest with 15-20 approximately equal spines; terminal spurs well developed, nearly as long as tarsal segments 1 + 2.

Identification. — *Bolbogonium impressum*, the largest species in the genus, has a single well-pronounced transverse tubercle on the middle of the frons, by which it is immediately separated from the other species in the *triangulum* group. *B. wiebesi* bears a similar frontal tubercle, but differs in shape of clypeus, sharpness of pronotal crest, general sculpture of dorsum, etc.

Material examined. — 6 specimens.

Holotype from Bengal (Copenhagen museum). Further specimens as follows.

India: Dehra Dun, leg. Asmadon (1); Pusa, i.1921, leg. Senior White (1♂), 16.ix.1916, leg. Fletcher (1♂); Simla, vii.1909 (1♀) (all BM); another specimen from Bengal without details (1♂, SMT), figured here.

***Bolbogonium scurra* sp. nov. (figs. 8, 22, 39)**

Description (holotype, male). — Approximate length 11, width 6, height 5 mm. Orange-yellow, shiny; tips, ridges, margins, sutures, punctures more or less infuscated; pilosity yellowish. Habitus, fig. 39.

Labrum long, emarginate in front, sides widely rounded, surface rugulate-punctate. Cephalic contours, fig. 8. Clypeus with distinctly raised anterior margin; lateral ridges distinct; surface irregularly rugulate-punctate. Frontal elevation situated immediately against clypeofrontal suture, which is slightly shifted forward; elevation consisting of a V-shaped saddle connecting a pair of infuscated tips; anterior declivity of elevation very steep, closely, finely punctate, posterior declivity gently sloping to vertex, punctate-rugulate; lateral declivity with similar sculpture. Disc of frontovertex virtually flat, very sparsely punctate, sides and posterior declivity of vertex more densely punctate; punctures approximately isodiametric, moderately defined, distinctly impressed, their diameters ca. 0.05 mm, densities centrally scarcely exceeding 5/0.1 sq. mm. Lateral delimitation of vertex formed by distinct, but not particularly raised, arcuate crest. Eye-canthus with raised anterior margin, sculpture punctate-rugulate, adjacent section of frontolateral ridge obsolescent. Maximum length of head (exclusive of labrum) 2.50, maximum width 3.15 mm; ratio 1/w 0.80.

Pronotal contours, fig. 22; anterior declivity of pronotum impressed, but lacking distinct horizontal base behind apical border; superior crest moderately pronounced, median protrusion distinct, discal midline shallowly impressed; anterolateral angles obtuse, posterolateral angles obsolete, widely rounded; base marginate. Pronotal punctation double; base of anterior declivity abundantly punctate, sides closely punctate; remaining surface also with abundant primary punctures, except around protrusion and on paramedian parts of disc, where secondary punctation is dominant; primary punctures large, isodiametric, distinctly impressed and generally well-defined; diameters of sublateral punctures ca. 0.07 mm (increasing laterad), their densities 7-10/0.25 sq. mm (increasing laterad); secondary punctures fine, isodiametric, sizes variant. Pronotal median length 3.1, maximum width 6.1 mm; ratio 1/w 0.50. Scutellum deltoid, finely punctate; micropunctures ( $\times 75$ ) present.

Juxtasutural punctures of elytron very distinct. Discal striae of elytron shallowly impressed; punctures infuscated, deeply impressed, exceedingly well-defined, isodiametric, locally irregularly spaced, their diameters ca. 0.05 mm; peripunctural impressions indistinctly affecting interstrial surface; stria 2 abbreviated behind. Interstriae very weakly convex, with numerous fine punctures, generally separated by a few times their diameters, which are ca. 0.07 mm.

Fore tibia with 7 external denticles, their size decreasing proximad; terminal spur well developed, reaching halfway tarsal segment 2. Femora all setose beneath, without notable details. Middle and hind tibiae with spinose fossorial elevations increasingly developed distad; number in right middle tibia 3 + (2), in right hind tibia also 3 + (2); crests of non-apical elevations arcuate; number of fossorial spines along crest of anteapical elevation on right middle tibia 12, all

approximately equal-sized; spurs of hind tibiae with rounded tip, not tapering, reaching segment 3 of tarsus.

Variation. — Length 8.5–11 mm. The three specimens at hand are, apart from the usual differences related to size, very similar.

Identification. — *Bolbogonium scurra* is close to *insidiosum*, from which it differs primarily by its flat vertex, its different V-shaped frontal elevation (the legs of the V being wide apart), and its trapeziform clypeus.

Material examined. — 3 specimens.

Holotype from South India: Coimbatore, vi.1966, leg. P.S. Nathan (Howden collection). Two paratypes, also from Coimbatore, xi.1966, leg. P.S. Nathan (Howden collection, L).

### ***Bolbogonium insidiosum* sp. nov. (figs. 9—12, 23, 40)**

Description (holotype, male). — Approximate length 8.5, width 5, height 3.5 mm. Yellow-brown, shiny; tips, ridges, margins, sutures, punctures more or less infuscated; pilosity yellowish. Habitus, plate 1.

Labrum emarginate in front, sides widely rounded, surface rugulate-punctate. Cephalic contours, fig. 9. Clypeus surface rugulate-punctate; sides limited by ridge, protuberant anteromedially. Frontal elevation situated immediately against clypeofrontal suture, which is slightly shifted forward; elevation U-shaped, anteriorly protuberant, on either side terminating at well-developed tubercle; interior surface of U punctate-rugulate, elevated; sides of frons punctate-rugulate as well; frontolateral ridge distinct. Vertex with large U-shaped, sparsely punctate impression, laterally limited by acute crest. Eye-canthus with raised anterior margin, surface indistinctly rugulate. Maximum length of head (exclusive of labrum) 2.10, maximum width 2.50 mm; ratio  $l/w$  0.85.

Pronotal contours, fig. 22; anterior declivity impressed, but without horizontal base behind apical border; superior crest moderately pronounced, median protrusion distinct, discal midline shallowly impressed; anterolateral angles obtuse, posterolateral angles obsolete, widely rounded; base marginate medially. Pronotal punctation generally sparse, double ( $\times 25$ ), more abundant on midline and lateral declivities; primary punctures large, isodiametric, distinctly impressed, generally well defined; their densities sublaterally 10–12/sq. mm, diameters somewhat less than 0.1 mm. Median length of pronotum 2.45, maximum width 4.75 mm; ratio  $l/w$  0.52. Scutellum deltoid, finely punctate; micropunctures ( $\times 75$ ) present.

Juxtasutural punctures of elytron distinct. Discal striae of elytron shallowly impressed; punctures large, deeply impressed, well defined, locally irregularly spaced, their diameters ca. 0.05 mm, separated by 2–4 times this diameter; peripunctural impressions slightly affecting interstrial surface; stria 2 extending onto posterior declivity. Discal interstriae weakly convex with fine punctures, generally separated by few times their diameter.

Fore tibia with 8–9 external denticles, their size decreasing proximad; terminal spur well developed, reaching halfway tarsal segment 2. Femora all setose beneath, without notable details. Middle and hind tibia with spinose fossorial

elevations, increasingly, developed distad; number in right middle tibia 2 + (3), in right hind tibia 3 + (2); crests of non-apical elevations arcuate; number of fossorial spines along crest of anteapical elevation on right middle tibia ca. 15; Spurs of hind tibiae with rounded tip, not tapering, reaching tarsal segment 3.

Variation. — Length 7—11 mm. This species is extremely variable in shape of clypeus, ornamentation of frons and vertex, development of the anteromedian protrusion of pronotum. The variation in the shape of the clypeofrons is illustrated in figs. 10—12.

Identification. — *Bolbogonium insidiosum* is recognizable by its frontal elevation and the characteristically impressed vertex. As stated in the preceding paragraph, variation is considerable.

The frons may be trituberculate with variably pronounced intervening ridges. The development of the tubercles themselves varies as well, the anterior one independently from the posteriors; in extreme cases only an arcuate ridge is left in front of the posterior pair of tubercles. The degree of impression of the vertex varies strongly, but remains noticeable, at least in the specimens I have seen. Compared to *scurra*, two useful features are the greater extension of elytral stria 2 and the frontal elevation not being a wide-legged V.

Material examined. — 33 specimens.

Holotype from India: Madras: Coimbatore, xi.1964, leg. P.S. Nathan, 1400 ft (M). Paratypes as follows.

India. — Bellary, 1896, De Morgan (1, P, mentioned by Boucomont, 1911: 340); Belgaum (1 ♀, BM); Chinchona, Anomalai Hills, v.1966, Nathan, 3500 ft (1 ♀, Schulze coll.); Coimbatore, xi.1955 (4, CNC), xi.1958 (1, Howden coll.), xi.1962 (1, CNC), x.1962 (2, CNC), xi.1963 (1 ♀, L), i.1964 (6, CNC), xii.1966 (6, Howden coll.), all Nathan, 1400 ft; Hoshangabad, 14-19.ix.1911, T.S.F. [?], at light (1 ♀, BM); Kadanpur [?, indistinct handwriting] (1 ♀, 1, SMT); Kadegaon (1 ♂, 1 ♀, BM, seen by Boucomont); Nagpur, 10.xii.1915 (1 ♀), 2.xii.1917 (1), 26.xii.1918 (1), d'Abreu (all BM); Buldana, Sagoda Purna, 7.iii.1930, Chatterjee (1, BM). A worn ♀ from „India bor.” (BM) excluded from type-series (mentioned by Boucomont, 1911: 341).

### ***Bolbogonium punctatissimum* (Westwood) comb. nov. (figs. 13, 21, 41)**

*Bolboceras punctatissimus* Westwood, 1852: 22, pl. 4 fig. 9, 9a (type-loc. Moradabad).

*Bolboceras punctatissimum*; Boucomont, 1912: 12 (in catalogue).

Description (holotype, not sexed). — Approximate length 8, width 5, height 4 mm. Brownish yellow, shiny; tips, ridges, margins, sutures more or less infuscated; pilosity yellowish. Habitus, fig. 41.

Labrum short, slightly emarginate in front, sides widely rounded, surface sculpture indistinct. Cephalic contours, fig. 13. Clypeal margins raised, particularly anteriorly, marginal ridge obsolete near rounded anterolateral angles; surface closely punctate, punctures small, somewhat irregular, shallow, weakly defined; interspaces not exceeding diameters of punctures, which are ca. 0.05 mm; clypeo-frontal suture laterally distinct. Middle of frons raised between genal angles, with

pair of low transverse elevations; punctation like that of clypeus, but generally closer, almost malleate-punctate; frontolateral ridge indistinct. Lateral delimitation of vertex not marginate, though still abruptly declivous; posterior surface of vertex concavely acclivous; sculpture like that of clypeus and frons. Eye-canthus with raised margin, sculpture like that of frons. Maximum length of head (exclusive of labrum) 1.8, maximum width 2.4 mm; ratio 1/w 0.79.

Pronotal contours, fig. 21; anterior declivity impressed; superior crest poorly pronounced, discal midline shallowly depressed, anterolateral angles obtuse, posterolateral angles obsolete, widely rounded; borders entirely marginate. Pronotal punctation double ( $\times 50$ ); base of anterior declivity and sides punctate-rugulate, remaining surface with close primary punctation; punctures small, shallow, locally ill-defined; diameters of discal punctures mostly slightly exceeding 0.05 mm, their densities 50-60/0.25 sq. mm; secondary punctures numerous, extremely fine. Median length 2.8, maximum width 4.7 mm; ratio 1/w 0.58. Scutellum deltoid, its surface punctate.

Juxtasutural punctures of elytron indistinct. Discal striae shallowly impressed; punctures slightly infuscated, small, shallow, regularly spaced, peripunctural impressions indistinctly affecting interstrial surface. Interstriae scarcely convex, with scattered primary punctures mostly separated by one or two times their diameters, which are ca. 0.025 mm; secondary punctation as on pronotum.

Fore tibia with 7 external denticles, their size decreasing proximad; terminal spur well developed, reaching to tarsal segment 3. Femora all moderately setose beneath, without notable details. Middle and hind tibiae with spinose fossorial elevations increasingly developed distad; number in right middle tibia 3 + (2) in right tibia 3 + (2); crests of distal elevations emarginate; number of fossorial spines along crest of anteapical elevation in right middle tibia 6 (superiorly) and ca. 9 (inferiorly), inferior spines longer than superior ones; spurs of middle tibia acuminate; those of hind tibia scarcely tapering, with rounded tip, nearly as long as tarsal segments 1 + 2.

Identification. — *Bolbogonium punctatissimum* is closely allied to *B. howdeni* but differs in frontal ornamentation and general sculpture of dorsum. These differences are rather tentative, since the type of *punctatissimum* is the only specimen known to me. Some forms in the *triangulum* group have also a pair of small frontal tubercles, but these are readily distinguished by the produced anterolateral angles of the clypeus.

Material examined. — Holotype only (BM), with label reading "Ind. or./Moradabad/on Evening/in the Ruins/by a Candle".

### ***Bolbogonium howdeni* sp. nov. (figs. 14, 24, 42)**

Description (holotype, male). — Approximate length 9, width 5, height 4 mm. Light brown, shiny; tips, ridges, margins, sutures more or less infuscated; pilosity yellowish. Habitus, fig. 42.

Labrum rather strongly protruding, almost rectilinear in front, sides rounded; surface rugulate-punctate. Cephalic contours, fig. 14. Clypeus shallowly concave behind raised front margin, lateral borders not distinctly raised; surface entirely

malleate-punctate; clypeofrontal suture indistinct. Raised clypeofrontal disc with 3 small but conspicuous tubercles between genal angles; frontal sculpture similar to that of clypeus; frontolateral ridge indistinct. Vertex closely punctate, punctures approximately isodiametric, small (diameters ca. 0.05 mm), shallow, but distinct. Eye-canthus with raised anterior margin, sculpture rugulate. Maximum length of head (exclusive of labrum) 1.80, maximum width 2.40 mm; ratio 1/w 0.76.

Pronotal contours, fig. 24; anteromedian declivity topped by distinct bisinuate crest; only surface immediately behind anteromedian border distinctly depressed; discal median longitudinal depression shallow; anterolateral angles obtuse, posterolateral angles obsolete, widely rounded; pronotal borders entirely marginate. Pronotal disc crowdedly punctate, punctures approximately isodiametric, well defined, of variable sizes, their diameters rarely reaching 0.1 mm; lateral declivities punctate-rugulate. Median length of pronotum 2.8, maximum width 5.1 mm; ratio 1/w 0.57. Scutellum deltoid, apex shortly arcuate; surface closely punctate.

Juxtasutural punctures of elytron weakly impressed. Striae on lateral declivity of elytron indistinct owing to strongly transversely wrinkled surface; punctures of striae 2 et seqq. poorly defined, regularly spaced, their diameters ca. 0.1 mm mostly separated by less than three times this diameter. Discal interstriae scarcely convex, with scattered small but distinct punctures, their diameters ca. 0.05 mm; micropunctuation hardly visible ( $\times 50$ ).

Fore tibiae with 7 external denticles; terminal spur well developed, reaching halfway segment 2. Femora all moderately setose beneath, without notable details. Middle and hind tibiae with spinose fossorial elevations increasingly developed distad; number in right middle tibia 3 + (1), in right hind tibia 3 + (2); crest of distal elevations emarginate; number of fossorial spines along crest of anteapical elevation ca. 4 (superiorly) and ca. 4 (inferiorly), their sizes variant; spurs of hind tibiae not tapering, with rounded tip, reaching approximately halfway tarsal segment 2.

Variation. — Length 9-11 mm. The four specimens at hand are, apart from the usual differences related to size, very similar.

Identification. — *Bolbogonium howdeni* is easily recognizable by the presence of three small tubercles on the frons and by its heavily sculptured dorsum (contiguously punctate, malleate-punctate, or punctate-rugulate). *B. punctatissimum* is certainly closely allied with *howdeni*, but clearly differs in the aforesaid characters.

Material examined. — 4 specimens.

Holotype from India: Bihar; Pachrukhi, 1927 (Howden collection); Howden correctly labelled it as being allied with *punctatissimum*. Paratypes from India: Chapra, leg. Mackenzie (1 ♀, BM); Pusa, 30.xi.1904 (1, BM). — Pakistan: Sind (1 ♀, P).

Note. — This species is dedicated to Dr. H. F. Howden, specialist in Geotrupidae, professor of biology at Carleton University, Ottawa.



***Bolbogonium wiebesi* sp. nov. (figs. 15, 25, 43)**

Description (holotype, male). — Approximate length 10, width 6.5, height 4.5 mm. Brown, shiny; tips, ridges, margins, sutures more or less infuscated; pilosity brownish. Habitus, fig. 43.

Labrum quite prominent, slightly emarginate in front, sides widely rounded, surface indistinctly rugulate. Cephalic contours, fig. 15. Front margin of clypeus strongly raised, forming a transverse costa; lateral limiting crests of horizontal surface obsolete. Frons with very weakly bifid transverse tubercle; clypeofrontal suture vaguely distinct laterally; frontolateral ridge indistinct. Eye-canthus with raised outer margin. Cephalic surface almost entirely malleate-punctate, impressions on posterior declivity of frontal tubercle somewhat transversely confluent; separate units medium-sized, their diameters just behind the eyes slightly over 0.05 mm. Maximum length of head (exclusive of mouthparts) 2.45, maximum width 2.40 mm; ratio  $l/w$  0.83.

Pronotal contours, fig. 25; anterior side with distinct impression topped by W-shaped crest; discal midline very shallowly impressed; anterolateral angles obtuse, posterolateral angles obsolete, widely rounded; borders entirely marginate. Pronotal punctation triple (magnification  $\times 50$ ); disc and anterior declivity with close primary punctation, punctures rather coarse, shallowly impressed though well defined, approx. isodiametric; their diameters ca. 0.07 mm, densities just beside midline ca.  $10/0.25$  sq. mm; density of primary punctures increasing laterad, marginal zone punctate-rugulate; secondary punctures discally most distinct, scattered, approximately isodiametric, diameters ca. 0.03 mm, densities beside discal midline almost  $20/0.25$  sq. mm; tertiary punctures numerous, moderately evenly distributed on pronotal disc. Median length of pronotum 3.4, maximum width 6.2 mm; ratio  $l/w$  0.55. Scutellum deltoid, with scarcely sinuate sides; surface with numerous distinct punctures, slightly smaller than primary ones of pronotal disc, diameters ca. 0.05 mm; secondary punctation dense, punctures resembling tertiaries of pronotal disc.

Juxtasutural punctures of elytron indistinct. Striae discally lightly impressed; punctures small, diameters scarcely exceeding 0.05 mm, separated by a few diameters; peripunctural impressions slightly affecting interstrial surface. Interstriae very slightly convex, punctation double; primary punctures scattered, distinct, approximately isodiametric, diameters less than 0.05 mm, separated by at least one diameter; secondary punctation remarkably close, punctures evenly distributed, fine, diameters less than one-tenth of the primary ones.

Fore tibia with 7 external denticles, their size decreasing proximad; terminal spur of fore tibia well developed, extending a little beyond tarsal segment 1. Femora all setose beneath, without notable details. Middle and hind tibiae with spinose fossorial elevations increasingly developed distad; number in right middle tibia 3 + (2); distal crests emarginate, number of fossorial spines along crest of anteapical elevation 5 (+ ca. 5 long setae) (superiorly), and 5 (inferiorly); spurs of middle tibia acuminate, those of hind tibia scarcely tapering, with rounded tip, slightly shorter than tarsal segments 1 + 2.

Identification. — *Bolbogonium wiebesi* is recognizable by the large frontal

tubercle; *impressum*, similar in this character, differs primarily by the produced anterolateral angles of its clypeus. In *wiebesi* the anterior margin of the clypeus is strongly costate; furthermore, the pronotal crest is remarkably sharp and the entire dorsum is heavily punctate.

Material examined. — Holotype only (BM), with labels reading "Burma/1919-103", "I/5".

Note. — This species is dedicated to Dr J. T. Wiebes, professor of systematic zoology and evolutionary biology at the State University of Leiden.

#### NOTES ADDED IN PROOF

Two recent descriptions of *Bolbogonium* extend the generic range (fig. 1) some hundreds of kilometers into Afghanistan. *Bolbogonium kabakovi* Nikolajev (1976: 693) from the Laghman province confirms the introductory notes given above under *B. triangulum* Westw., and I suspect a synonymy here. *Bolbogonium kabolicum* Nikolajev & Kabakov (1977: 646) from Kabul would easily key to point 7 in my key, and then seems immediately recognizable by its peculiar frontal ornamentation (l.c.: fig. 1).

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## APPENDIX

CHARACTERS AND CHARACTER STATES RELEVANT TO A SUPRASPECIFIC CLASSIFICATION OF THE TRIBE BOLBOCERATINI <sup>1)</sup>*Head (dorsal)*

- 1 (a) Outline of mandibles (outer margins) symmetrical.
- (b) Outline of mandibles (outer margins) asymmetrical.
- 2 (a) Outer margin of right mandible sinuate, poorly lobed, or simply arcuate.
- (b) Outer margin of right mandible, for the greater part, straight, or nearly so
- (c) Outer margin of right mandible with distinct arcuate lobe.
- (d) Outer margin of right mandible with distinct acute lobe.
- 3 (a) Transverse ridge of labrum present and distinct.
- (b) Transverse ridge of labrum absent, obsolete, or at least indistinct.
- \*4 (a) Outline of clypeus in dorsal view (male) approximately trapeziform.
- (b) Outline of clypeus in dorsal view (male) approximately semicircular.
- (c) Outline of clypeus different from preceding alternatives, e.g., very strongly modified by marginal protrusion(s) — to be specified for each case.
- \*5 (a) Perimarginal ridge of clypeus present and unmodified.
- (b) Perimarginal ridge of clypeus present and modified — but different from alternative (d).
- (c) Perimarginal ridge of clypeus entirely or largely obsolete.
- (d) Perimarginal ridge transformed into X-shaped ridges (dorsal view), cross-point with or without tubercle.
- \*6 (a) Base of any cephalic protrusion(s) restricted to clypeus, frons, or vertex, or situated on clypeofrontal transition.
- (b) Base of usually well-developed cephalic protrusion largely covering both clypeus and frons.
- 7 (a) Clypeus lacking single anteromarginal protrusion.
- (b) Clypeus with single anteromarginal protrusion — but not as sub character state 4 (c).
- \*8 (a) Clypeal disc with transverse ridge or pair of isolated elevations.
- (b) Clypeofrontal transition (suture) with transverse ridge or pair of isolated elevations.
- (c) Clypeal disc with a single tubercle — but not as sub character state 6 (b).
- (d) Clypeofrontal transition (suture) with a single tubercle — but not as sub character state 6 (b).
- \*9 (a) Frontal disc with transverse ridge or pair of isolated elevations.
- (b) Frons with pair of distinct para-ocular protrusions.
- (c) Frons or vertex with a single tubercle.
- 10 (a) Frontovortex lacking distinct impression(s), at most shallowly concave.
- (b) Frontovortex with distinct impression(s).
- \*11 (a) Vertex lacking transverse ridge.
- (b) Vertex with distinct transverse, straight or arcuate ridge.
- \*12 (a) Vertex not sharply separated from tempora.
- (b) Vertex separated from tempora by ridge.
- \*13 (a) Tempora not produced.
- (b) Tempora more or less produced, angulate.
- 14 (a) Vertex gently sloping to pronotal apex.
- (b) Vertex posteriorly limited by vertical declivity.
- 15 (a) Anterior margin of eye-canthus simply arcuate.
- (b) Anterior margin of eye-canthus straight, shortly rounded or with lateral angle and/or tubercle.
- \*16 (a) Eye-canthus and temporal lobe separated.
- (b) Eye-canthus and temporal lobe contiguous, dividing eye in two parts.
- 17 (a) Dorsally visible area of eye small — to be specified for each case.
- (b) Dorsally visible area of eye large — to be specified for each case.

<sup>1)</sup> Characters suggested to be of primary diagnostic importance are marked with an asterisk.

*Pronotum (male) and scutellum*

- 18 (a) Pronotum lacking distinct non-marginal protrusions, simply convex (except for shallow median longitudinal sulcus).
- (b) Pronotum with distinct non-marginal protrusions — characters 19—22 conditional on this character state.
- \*19 (a) Pronotum simply retuse anteromedially, declivity surmounted by transverse discal crest; lacking discal paramedian or lateral protrusions.
- (b) Pronotum distinctly concave anteromedially, but lacking transverse discal crest or any other protrusions.
- (c) Pronotum with pairs of paramedian and/or lateral protrusions (usually tubercles); in well-developed forms frequently with anteromedian and/or sublateral impressions.
- \*20 (a) Pronotum lacking crest just behind apex proceeding onto lateral declivities.
- (b) Pronotum with crest just behind apex proceeding onto lateral declivities.
- \*21 (a) Pronotum not, at the same time, with sharp posterior crest running roughly parallel to base, and anterior surface retuse to strongly concave.
- (b) Pronotum with sharp posterior crest running roughly parallel to base, and anterior surface retuse to strongly concave.
- 22 (a) Pronotal protrusion(s) not restricted to basal area.
- (b) Pronotal protrusion(s) restricted to basal area.
- \*23 (a) Pronotal apex lacking pair of small deep impressions.
- (b) Pronotal apex with pair of small deep impressions (bifoveate).
- 24 (a) Pronotal base marginate (at least medially).
- (b) Pronotal base immarginate.
- \*25 (a) Pronotal apex medially marginate or immarginate, but unmodified.
- (b) Pronotal apex modified (e.g., tuberculate or with high transverse ridge).
- 26 Conditional on 25 (b).
- (a) Pronotal apex unituberculate (in one known case with long upbent horn).
- (b) Pronotal apex bituberculate, occasionally tubercles confluent or obsolescent.
- (c) Pronotal apex strongly elevated over much of its width (costate or carinate).
- 27 (a) Pronotal apex fringed with narrow velum and/or setae.
- (b) Pronotum lacking velum, but fringed with long setae.
- \*28 (a) Scutellum semicircular, semielliptic, sides may be more or less parallel or weakly sinuate in front — character state 29(c) excepted.
- (b) Scutellar sides strongly sinuate (curving laterad in front) — character state 29(c) excepted.
- (c) Scutellum simply triangular.
- (d) Shape of scutellum different form preceding alternatives — to be specified for each case.
- \*29 (a) Scutellum very wide ( $1/w < 1$ ).
- (b) Scutellum short ( $1/w \approx 1-2$ ).
- (c) Scutellum elongate ( $1/w \geq 2$ ).

*Elytron*

- \*30 (a) Elytral base immarginate.
- (b) Elytral base marginate (ridged).
- 31 (a) Elytral epipleuron reaching apico-sutural angle.
- (b) Elytral epipleuron obsolete at some distance from elytral apex (at the beginning of the distal curve).
- \*32 (a) Elytron with 7 striae between suture and humeral umbone.
- (b) Elytron with 5 striae between suture and humeral umbone.
- (c) Elytron with 9 striae between suture and humeral umbone.
- 33 (a) Stria 5 extending to (near) elytral base.
- (b) Stria 5 obsolete in front.
- \*34 (a) Stria 1 terminating at side of scutellum, stria 2 interrupted in front or reaching base of elytron (not basal angle of scutellum).
- (b) Both striae 1 and 2 terminating at side of scutellum (2 occasionally terminating at basal angle of scutellum).

- (c) Stria 1 proceeding to elytral base.
- 35 (a) Elytral striae 2—7 not or only scarcely impressed, intervals (= interstriae) not or only scarcely convex.
- (b) Elytral striae sulcate, intervals distinctly convex.
- 36 Conditional on 35(b).
- (a) Elytral intervals all approximately equally convex.
- (b) Odd intervals of elytral disc (at least juxtasutural one) much more convex than even intervals.
- 37 (a) Humeral angle of elytron unmodified.
- (b) Humeral angle of elytron tuberculate.

### *Antenna*

- 38 (a) Antennal club normal, not thicker than length of pedicel and subsequent flagellar segments combined.
- (b) Antennal club very robust, thicker than length of pedicel and subsequent flagellar segments combined (outer surface of ultimate segment usually distinctly convex).
- \*39 Conditional on 38 (b).
- (a) Distal side of club segment 3 evenly convex or nearly so.
- (b) Distal side of club segment 3 remarkably swollen near base.
- \*40 (a) Proximal surface of club segment 1 entirely pubescent, lacking glabrous, polished area.
- (b) Glabrous, polished area on proximal side of club gradually passing to pubescent parts.
- (c) Glabrous, polished area on proximal side of well separated from remaining, pubescent surface.
- \*41 (a) Distal side of club segment 3 lacking grooves.
- (b) Distal side of club segment 3 with 2 distinct grooves.

### *Pectus*

- 42 (a) Anterior paramedian costae of prosternum distinct.
- (b) Anterior paramedian costae of prosternum obsolete.
- 43 Conditional on 42 (a).
- (a) Prosternum convex or flat (occasionally wrinkled) between anterior paramedian costae.
- (b) Prosternum with median longitudinal ridge, but juxtacoxal surface not deeply concave.
- (c) Prosternum, behind anterior paramedian costae, with longitudinal costa limited by deep juxtacoxal holes.
- (d) Prosternum sulcate (not simply concave) between anterior paramedian costae.
- 44 (a) Prosternum lacking any posteromedian protrusion, not even a longitudinal ridge.
- (b) Prosternum with some posteromedian protrusion.
- 45 Conditional on 44 (b).
- (a) Prosternum lacking posteromedian spine or similar protrusion.
- (b) Prosternum angulate, or with isolated posteromedian spine or similar protrusion.
- \*46 Conditional in 44 (b).
- (a) Prosternum not bulbose or otherwise inflated-dilated.
- (b) Prosternum bulbose posteromedially.
- (c) Prosternum with well-developed lanceolate posteromedian process.
- (d) Prosternum with transverse, bidentate posteromedian process.
- \*47 (a) Middle coxae (sub)contiguous, anteromedian process of metasternum indistinct.
- (b) Middle coxae distinctly separated, although anteromedian process of metasternum may be strongly narrowed.
- 48 Conditional on 47(b).
- (a) Metasternal process between middle coxae not strongly narrowed.
- (b) Metasternal process between middle coxae strongly narrowed.
- \*49 Conditional on 47(b).
- (a) Metasternal disc pyriform in outline.
- (b) Metasternal disc rhomboid in outline.
- (c) Metasternal disc different from preceding alternatives — to be specified for each case.

- \*50 Conditional on 47(b).
- (a) Metasternal process flat, or nearly so, abruptly retuse in front, with complete perimarginal ridge, adjacent mesosternal declivity more or less concave.
  - (b) Metasternal process flat, or nearly so, abruptly retuse in front, lacking perimarginal ridge, adjacent mesosternal declivity more or less concave.
  - (c) Metasternal process long and narrow (linear), but not reduced to a sharp carina.
  - (d) Metasternal process gradually passing to mesosternum, not limited by some transverse protrusion, lacking longitudinal carina.
  - (e) Metasternal process with distinct median longitudinal carina, which may be more or less angulate in front (prow-shaped).
  - (f) General surface of metasternal process hunched, different from preceding alternatives.
- \*51 Conditional on 47(b).
- (a) Metasternal process lacking any particular accessory protrusions.
  - (b) Metasternal process with robust denticle in front.
  - (c) Metasternal process with fine spine or hook in front.
- 52 (a) Mesometasternal suture noticeable at base of declivity.
- (b) Mesometasternal suture obsolete.
- 53 (a) Longitudinal suture of metasternum (largely) obsolete.
- (b) Longitudinal suture of metasternum distinct.

#### *Abdomen*

- 54 Structure of stridulatory organ — available data insufficient for classification.

#### *Legs (male)*

- 55 (a) Fossorial elevations of middle and hind tibiae with straight, angulate — emarginate, bidentate, of bilobate crest (reference: anteapical elevation of hind tibia).
- (b) Fossorial elevations of middle and hind tibiae with arcuate crest (reference: ditto).
- 56 (a) Middle tibia with a single non-apical fossorial elevation, others completely obsolete or noticeable only as pairs of isolated denticles.
- (b) Middle tibia with two or more complete non-apical fossorial elevations.
- 57 (a) Fore tibia normal.
- (b) Fore tibia strongly dilated.
- \*58 (a) Femora indentate.
- (b) Femora deatate (particularly fore femora).
- \*59 (a) Terminal spur of fore tibia long and slender, scarcely tapering.
- (b) Terminal spur of fore tibia more or less triangular, with acute apex, occasionally very robust.
- \*60 (a) Tarsal segment 1 of fore-legs short.
- (b) Tarsal segment 1 of fore-legs remarkably elongate.

#### *Genitalia*

- \*61 (a) Aedeagus consisting of two parameres.
- (b) Separate parameres indistinct.
- 62 Conditional on 61 (a).
- (a) Parameres strongly sclerotized, without notable accessory elements.
  - (b) Parameres sclerotized and strongly modified, i.e. with accessory elements.
  - (c) Parameres very small, poorly sclerotized, without notable accessory elements.
  - (d) Different from preceding alternatives — to be specified for each case.

#### *Sexual dimorphism*

- 63 (a) Armature (sculptural ornamentation) of head and pronotum of male and female belonging to the same species similar.
- (b) Armature (sculptural ornamentation) of head and pronotum of male and female belonging to the same species radically different — to be specified, see characters 4 et seq., 18 et seq.

*Colours*

- 64 (a) Colour uniform throughout, apart from infuscated ridges, sutures, tips, margins, punctures, etc.  
(b) Colour not uniform throughout.
- 65 Conditional on 64(a).  
(a) Colour some lighter tone of brown.  
(b) Colour some very dark tone of brown, or black.
- 66 Conditional on 64(b).  
(a) Elytra and pronotum differently, but uniformly coloured.  
(b) Elytra and/or pronotum with some colour pattern.



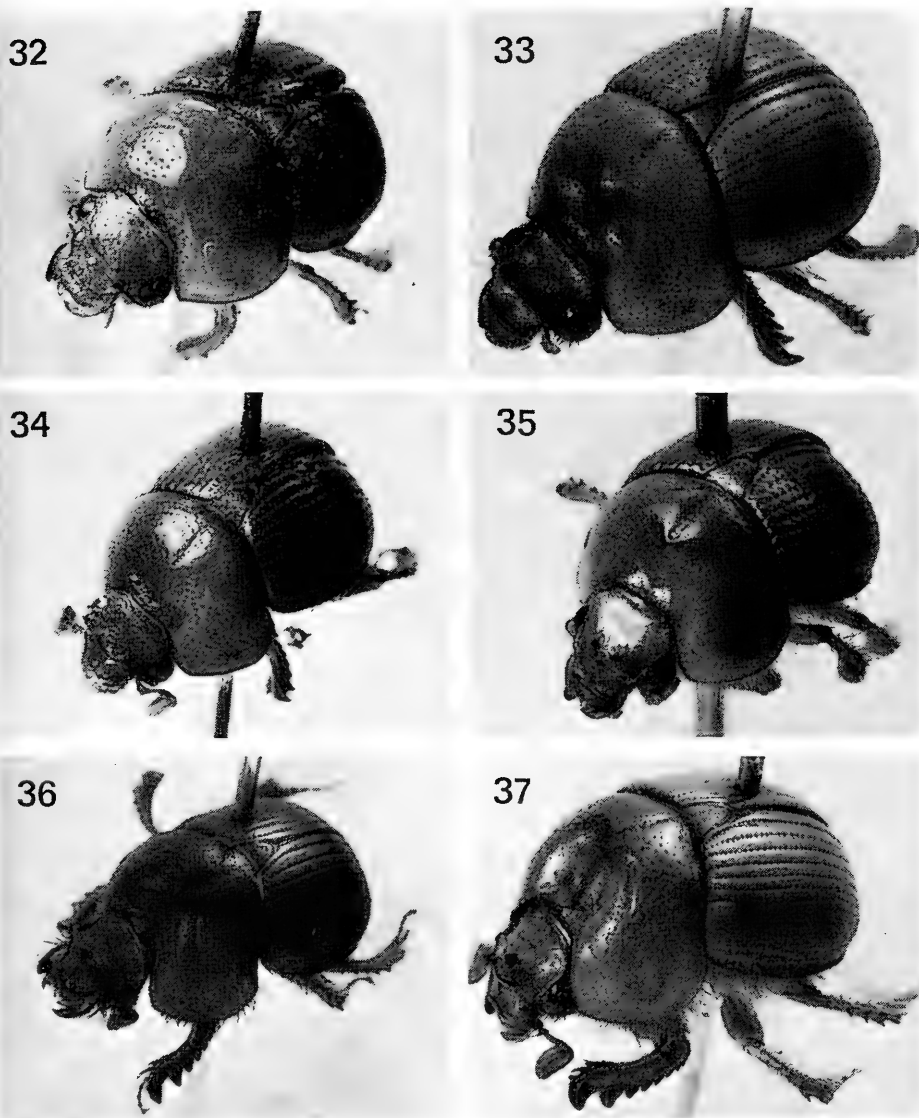


Plate 2. *Bolbogonium* species. 32, *addendum*, holotype; 33, *bicornutum*, holotype; 34, *pseudopunctatissimum*, holotype; 35—37, *triangulum*, ♂ Tarnab (35), ♂ Burma (36), ♀ Kanpur (37), length ca 8, 11.5, 11 mm, respectively.

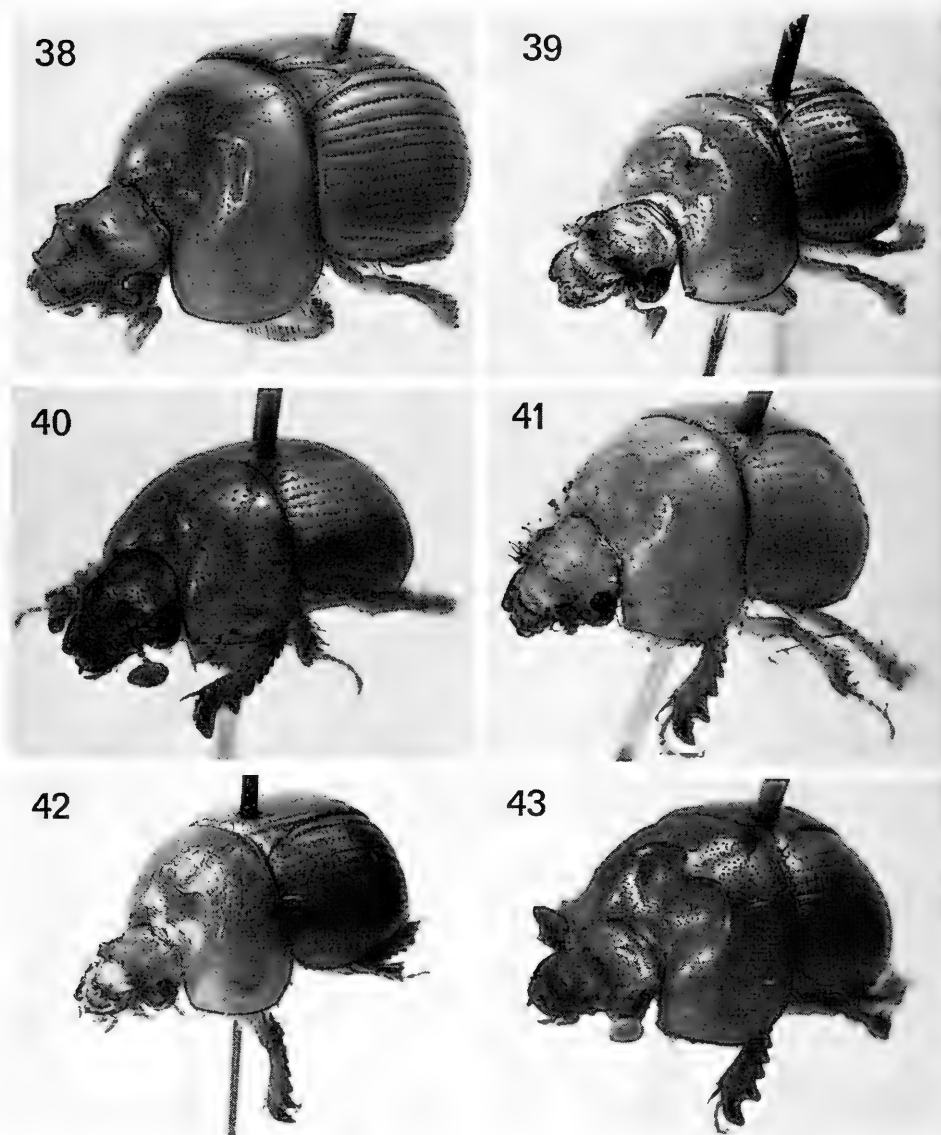


Plate 3. *Bolbogonium* species. 38, *impressum*, ♂ Bengal, length 12.5 mm; 39, *scurra*, holotype; 40, *insidiosum*, holotype; 41, *punctatissimum*, holotype; 42, *howdeni*, holotype; 43, *wiebesi*, holotype.









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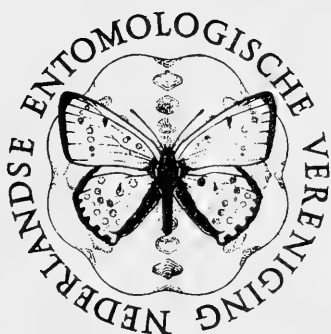
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# TIJDSCHRIFT VOOR ENTOMOLOGIE

UITGEGEVEN DOOR

DE NEDERLANDSE ENTOMOLOGISCHE VERENIGING



## INHOUD

- F. WILLEMSE. — A study on the genus *Cranaella* Ramme (Orthoptera, Acridoidea, Catantopinae), p. 109—120, text-figs. 1—30, pl. 1. — A study on the genus *Cranae* Stål (Orthoptera, Acridoidea, Catantopinae), p. 121—152, text-figs. 1—45, pls. 1—5.





# A STUDY ON THE GENUS *CRANAELLA* RAMME (ORTHOPTERA, ACRIDOIDEA, CATANTOPINAE)

by

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With 30 text-figures and one plate

## ABSTRACT

Morphological characters of all previously recognized species of the genus *Cranaella* Ramme are given, together with the descriptions of three new species: *kevani*, *rammei*, and *samarensis*. A key is given to the species of this genus, which occurs in the Philippines and Celebes.

## INTRODUCTION

Material of *Cranaella* is scarce. Ramme, when creating this genus, recorded four adult females and one juvenile male, representing three new species: *carnipes*, *tuberculata* and *willemsei*. C. Willemse (1956) mentioned another two females and two males, one male as *willemsei*, the other specimens as *tuberculata*. Kevan (1966) recorded another two males and one female as *tuberculata* and described a fourth species, *multicolor*, after a single female. Before me I have a collection of 30 males and 17 females. In the present study morphological characters, especially of the genitalia, are given, and three new species are described.

Depositories of the material are given throughout the text in abbreviated form:

ANSP Academy of Natural Sciences of Philadelphia, U.S.A.;

BPBM Bernice P. Bishop Museum, Honolulu, Hawaii;

NMM Natuurhistorisch Museum, Maastricht, Netherlands;

ZMHU Zoologisches Museum der Humboldt-Universität, Berlin, Germany.

My thanks are due to the following persons: J. L. Gressitt and the late Miss S. Nakata, Honolulu; K. K. Günther, Berlin; H. Radclyffe Roberts and D. Rentz, Philadelphia.

## *Cranaella* Ramme

*Cranaella* Ramme, 1941: 94, 217, 226, 241; C. Willemse, 1956: 9, 108.

Type-species: *Cranaella carnipes* Ramme, 1941.

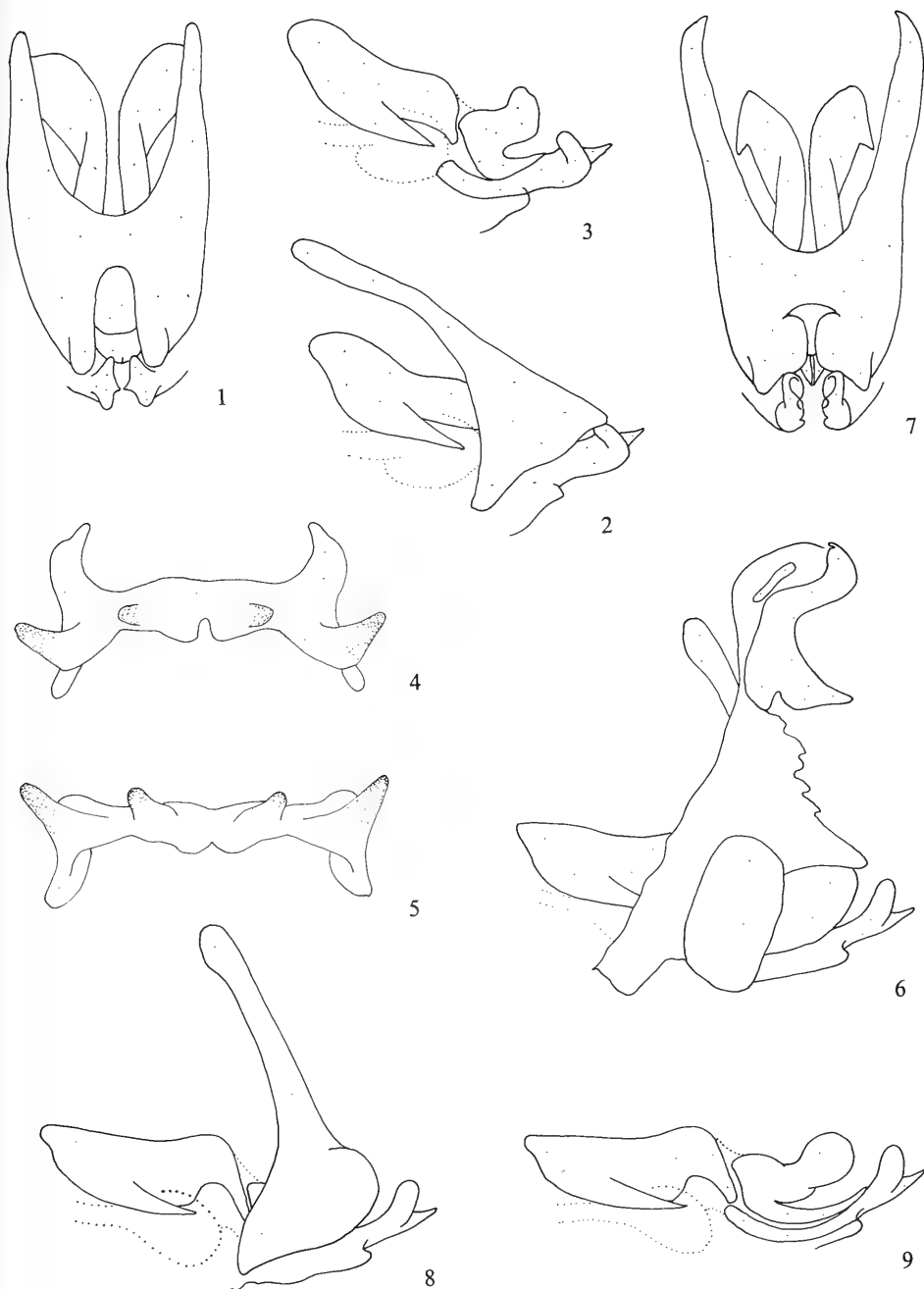
*Cranaella* belongs to the *Cranae* group of genera, preliminarily arranged under the subfamily Catantopinae. In the original description it is said that *Cranaella*

differs from *Cranae* Stål in the rougher sculpturation of head and thorax, the less strongly developed pronotal sulci and narrower elytra, with the hind margin (not "Vorderrand") slightly concave. However, as to these points the discontinuity between these genera is merely gradual. Also the genitalia are much the same in both genera. It is not within the scope of the present study to discuss the status of the genera of the *Cranae* group. Therefore I abstain from redescribing *Cranaella* more definitely. However, phenetic relationships of *Cranaella* species both mutually as well as with species of the *Cranae* complex (s.l.) are pointed out here.

In *Cranaella*, specific characters may be found in the apex of the phallus and the hind margin of the last abdominal tergite in the male, in the subgenital plate in the female and in the sculpturation of the hind femur, in the shape of the prosternal process, in the development of the hind wing and the shape of the elytron, and in the coloration in both sexes.

### Key to the species of *Cranaella*

1. Hind femur sanguineous (Celebes) . . . . . *carnipes* Ramme (p. 112)
- Hind femur not red (Philippine Is.) . . . . . 2
2. Elytron wider, about two-and-one-half times as long as wide, yellowish green without black venation, reaching the margins . . . . . *multicolor* Kevan (p. 119)
- Elytron narrower, three times or more as long as wide, venation by far not reaching the (slightly transparent) margins, the area of venation black . . . . . 3
3. Ridges of the fishbone pattern of the outer medial area of the hind femur of same colour as the hind femur; each ridge with an, often black, tubercle near the lower and usually also near the upper carinulae; prosternal process widened laterally, lateral edge of apex slightly conical; hind wing vestigial . . . . . 4
- These ridges in black, contrasting with the colour of the hind femur and without tubercles; prosternal process almost cubical, lateral edges of the apex not conical; hind wing present, although shorter than the elytron . . . . . 5
4. Hind margin of last abdominal tergite in male not or slightly incised in the middle, without furculae (fig. 20); apex of phallus with distal part distinctly marked off from the proximal part of the apex (figs. 10—11) . . . . .
- . . . . . *tuberculata* Ramme (p. 112)
- This margin with a pair of small and widely separated furculae (fig. 21); apex of phallus with distal part gradually merging in the proximal part (figs. 12—13) . . . . .
- . . . . . *kevani* sp.n. (p. 115)
5. Hind margin of the last abdominal tergite in male shallowly emarginate in the middle, without furculae (fig. 22); apex of phallus with short distal part (figs. 14—15) . . . . . *willemsei* Ramme (p. 116)
- This margin with a narrow incision in the middle and a pair of furculae (figs. 23—24); distal part of apex of phallus longer (figs. 16—19) . . . . . 6
6. Distal part of apex of phallus comparatively long (figs. 16—17) . . . . .
- . . . . . *rammei* sp.n. (p. 118)
- Distal part of apex of phallus comparatively short (figs. 18—19) . . . . .
- . . . . . *samarensis* sp.n. (p. 118)



Figs. 1—5. *Cranaella tuberculata* Ramme, ♂, Surigao, phallic complex: 1, dorsal view, ectophallic membrane and epiphallus removed; 2, the same, lateral view; 3, endophallus, lateral view; 4, epiphallus, dorsal view; 5, the same, posterior view. Figs. 6—9. *Cranaella willemsei* Ramme, ♂, Surigao, phallic complex: 6, lateral view; 7, the same, epiphallus and ectophallic membrane removed, dorsal view; 8, the same, lateral view; 9, endophallus, lateral view.

***Cranaella carnipes* Ramme, 1941**  
(fig. 25)

*Cranaella carnipes* Ramme, 1941: 94, 217, 228, pl. 14 fig. 3; C. Willemse, 1956: 108, 109.

This species is known from the type-specimens, an adult female (holotype) and a juvenile male (paratype). Both are labelled: Celebes Ile Ile 500 m 11.12.1930 G. Heinrich (ZMHU). Ramme's description is extremely short; his description of the coloration refers to the juvenile male; that of the holotype was given by C. Willemse.

Morphological characters of the holotype are as follows: integument finely pitted, impressions closely set; prosternal process widened laterally, lateral edges slightly conical; elytron about three times as long as wide, hind wing vestigial; ridges of outer medial area of hind femur not tuberculate; subgenital plate (fig. 25) flattened ventrally and depressed apically, hind margin tridentate with the lateral points almost as wide and long as the median point.

The juvenile male has the hind margin of the last abdominal tergite with a pair of small, triangular and widely separated furculae, resembling those of *kevani*. The tegmina are not yet developed. The phallic complex is so poorly sclerotized that details cannot be given.

Although the prosternal process and the tegmina are much as in *tuberculata* and *kevani*, the relationship of *carnipes* remains an open question by lack of an adult male.

***Cranaella tuberculata* Ramme, 1941**  
(figs. 1—5, 10—11, 20, 26, pl. 1 figs. 1—2)

*Cranaella tuberculata* Ramme, 1941: 95, 217, pl. 13 fig. 6; C. Willemse, 1956: 108, 109.

Material studied: Surigao, Mindanao, Baker 4♂ 3♀; Surigao, P.I., 9.vi (1♀) & 9.v.1916 (1♂); Surigao, Mindanao 2♂ 1 juv. ♂, 2♀ 1 juv. ♀; Iligan, Mindanao, Baker 1♂; Butuan, Mindanao, Baker 1♂ 1♀; Bucas, Philipp. 1♂; Siargao, Philipp. 1♀; Island Samar, Baker 2♂ 1♀; Isl. Biliran, Philippines, Baker 1♂; Dagami, Leyte, P.I., Mt. Lobi 21 (1♂) & 25 (1♀) & 26.vi (1♀) & 4 (2♂) & 10.viii (1 juv. ♂) & 26 (1♂) & 27.ix.1945 (1♀), E. R. Helwig (all ANSP, except 1♂ 2♀ from Surigao in NMM).

This species was described after the female holotype from Mindanao and a female paratype from Siargao. A description of the male characters was given by C. Willemse after a male from Surigao (Mindanao). The redescription which follows here is made after (topotypic) material from Mindanao.

**Redescription.**

♂, pl. 1 fig. 1. Integument of face, cheeks, thorax and dorsal sides of proximal abdominal tergites evenly and strongly pitted. Head as long as the pronotum. Pronotum with four transverse sulci, the fourth one located at about 5/6 of the length of the middle of the dorsum; posterior margin of dorsum broadly emarginate; lateral lobe 1/4 longer than high, posterior angle slightly produced

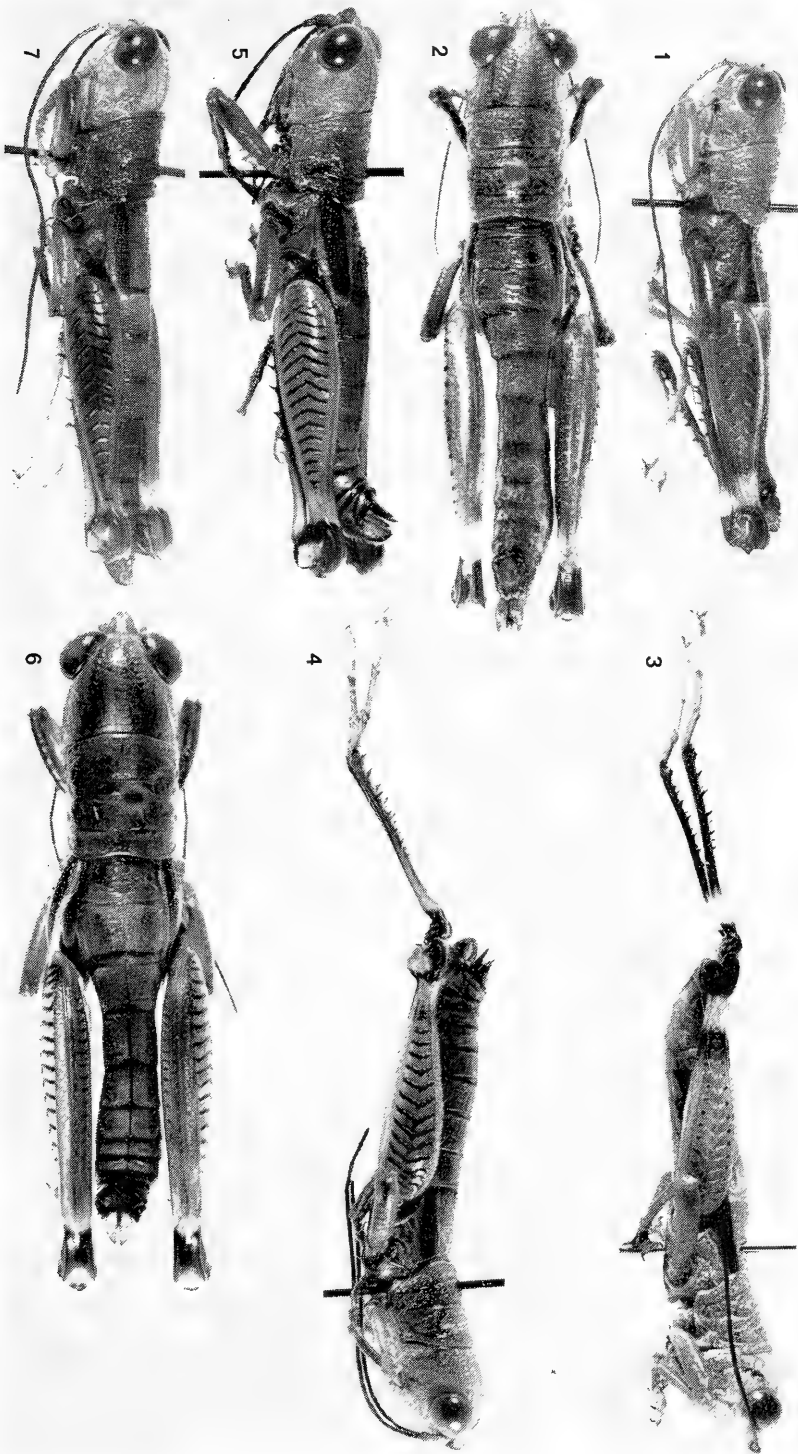


Plate 1, figs. 1—7. *Cranaella* species: 1, *tuberculata* Ramme, ♂, Surigao; 2, idem, ♀, Surigao; 3, *kevani* sp.n., ♂ holotype; 4, *willemsei* Ramme, ♂, Dinagat; 5, *rammei* sp.n., ♂ paratype; 6, idem, ♀ paratype; 7, *samarensis* sp.n., ♂ holotype.

posteriorly, ventral and posterior margins sigmoid. Prosternal process strong, vertical, slightly widened laterally, anterior side slightly longer than posterior one, ventral side flattened with the anterior margin straight or slightly convex, the posterior margin strongly convex, being curved towards the anterior margin, the lateral edges slightly produced conically. Elytron narrow, three to three-and-one-half times as long as wide, venation strongly reduced and confined to the middle area; the broad margins almost completely transparent, anterior margin slightly convex, posterior margin slightly concave, both margins about parallel, apex broadly rounded. Hind wing vestigial. Tympanum open, almost circular, on level with the body surface. Outer side of hind femur with the carinulae slightly tuberculate and the lower and upper ends of the ridges of the fishbone pattern more conspicuously tuberculate. Brunner's organ present. Lower inner carinula pilose.

Hind margin of the last abdominal tergite (fig. 20) widely concave, slightly thickened near the middle and shortly and narrowly incised in the very middle. Supra-anal plate (fig. 20) wider than long. Phallic complex and epiphallus as in figs. 1—5. Apex of phallus (figs. 10—11) with the ventro-posterior side strongly concave and the distal part of the apical penis valve distinctly marked off from the proximal part of the apex by a lateral collar-shaped fold.

General colour yellowish or reddish-brown. Antennae bluish-black, apical segments slightly paler, basal segments coloured as the head. Head of general colour or olivaceous green, clypeus with a median black dot and its lateral angles black. Thorax of general colour except for the ventral side of the prosternal process, the posterior margin of the pro- and the lateral margins of the mesosterna, which are bluish. Elytron with the area of venation black or dark blue. Abdomen of general colour, last tergite, cercus and margins of the supra-anal plate dark brown or blue. Fore and middle legs and hind femur of general colour or more reddish. Hind femur with the tubercles of the ridges of the fishbone pattern black; the lower inner marginal area bluish; a yellow or greenish antegenicular ring, often bordered with black proximally. Hind knee bluish-black, apex of the lobes yellowish and crescents castaneous-brown. Hind tibia and its condylus bluish-black, with a yellow postgenicular ring; spines with tips black. Hind tarsus bluish-brown, ventral side paler.

♀, pl. 1 fig. 2. Larger than male. Ventral side of subgenital plate depressed in the middle, the depression bordered laterally by a pair of strong and posteriorly slightly divergent keels, giving rise to a tridentate hind margin with the lateral points smaller than the median point (fig. 26). Coloration as the male.

Measurements (length in mm): body, ♂ 21.1-25.2, ♀ 23.5-32.0; pronotum, ♂ 3.8-4.3, ♀ 4.9-5.9; elytron, ♂ 4.1-4.5, ♀ 4.9-6.0; hind femur, ♂ 11.1-12.1, ♀ 13.0-15.5.

Distribution: Philippine Is. (Mindanao; Bucas; Siargao; Samar; Leyte; Biliran).

Discussion. The species is well-defined by the male genitalia. Among the material at hand, morphological characters vary but slightly. However, as to the coloration, the material from Samar and that from Leyte and Biliran is different from that of Mindanao. The pronotum of the Samar specimens has two black dots,

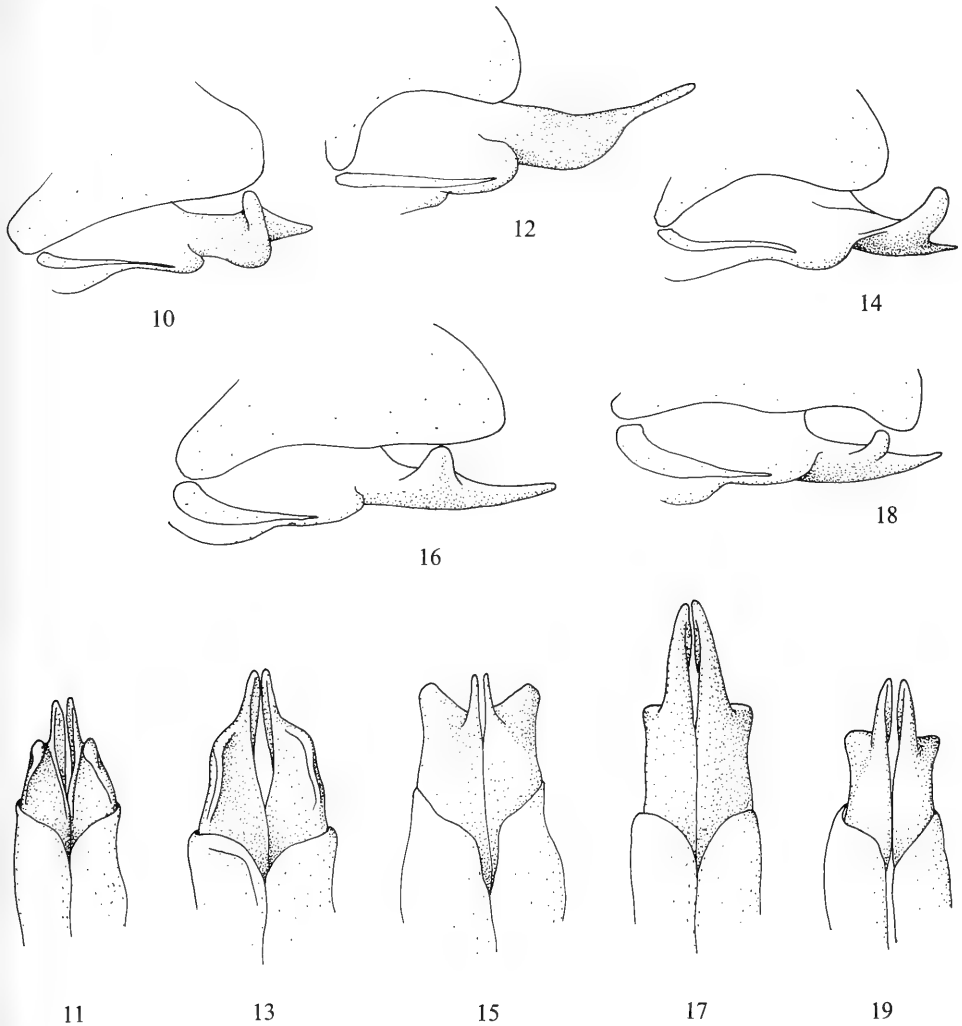
at the lateral ends of the second transverse sulcus. The material from Leyte and Biliran shows more or less numerous black dots scattered over the head and pronotum and almost unicolorous tubercles of the outer medial area of the hind femur.

***Cranaella kevani* sp.n.**

(figs. 12—13, 21, 27, pl. 1 fig. 3)

*Cranaella tuberculata* (nec Ramme); Kevan, 1966: 411.

Material studied: ♂ holotype, ♀ allotype, labelled: P.I., Misamis Or., Mt.



Figs. 10—19. *Cranaella* species, ♂, apex of phallus in ventro-posterior (odd numbers) and lateral (even numbers) view: 10—11, *tuberculata* Ramme, Surigao; 12—13, *kevani* sp.n., Calian; 14—15, *willemsei* Ramme, Surigao; 16—17, *rammei* sp.n., paratype; 18—19, *samarensis* sp.n., holotype.

Empagatao, 1050—1200 m, 19-30.iv.61, H. Torrevillas collector; paratypes: P.I., Misamis Or., Minalwang, 1050 m, 24.iii-4.iv.1961, W. Torrevillas 1♂ (all three specimens BPBM and labelled: *Cranaella tuberculata* Rm det.D.K.McE.Kevan 1965); Calian, Davao Prov., Mindanao, P.I., 10.v.1930, C. F. Clegg 1♂; Island of Basilan, Baker 2♂ 1♀ (ANSP).

### Description.

♂, pl. 1 fig. 3. Differs from *tuberculata* as follows. Pronotum slightly shorter, posterior margin of dorsum slightly emarginate. Hind margin of last abdominal tergite emarginate in the middle, with a pair of short and well separated furculae (fig. 21). Distal part of the apical penis valve not strongly marked off but more gradually merging in the proximal part of that valve (figs. 12—13).

Coloration as in *tuberculata*.

♀. Larger than male. Subgenital plate resembling that of *tuberculata*, but the keels slightly closer together (fig. 27). Coloration as in male, slightly more obscurely brownish.

Measurements (length in mm): body, ♂ 21.1-24.8, ♀ 27.0-30.9; pronotum, ♂ 4.0-4.1, ♀ 5.0-5.3; elytron, ♂ 3.8-4.6, ♀ 4.5-5.5; hind femur, ♂ 11.6-13.0, ♀ 13.9-15.0.

Distribution: Philippine Is. (Mindanao; Basilan).

Discussion. The species is well-defined by the male genitalia. The furculae may be slightly more widely separated than in the holotype. Specimens from Basilan differ slightly in the smaller measurements, the presence of a black dot at either end of the second transverse pronotal sulcus, and the unicolorous elytron in the female.

The material from Misamis Or. had been referred to *tuberculata* by Kevan. In that paper, the locality of the firstly recorded male (now paratype) is erroneously given similar to that of the following couple (now holo- and allotype).

Within the genus, *tuberculata* and *kevani* form a group characterized by the shape of the prosternal process, vestigial hind wing, tuberculated ridges of the fishbone pattern of the hind femur, and the appearance of the apex of phallus. As to the latter, especially in *kevani*, resemblance with the apex of phallus in *Cranae patagiata* Stål (type-species of that genus) is obvious.

### *Cranaella willemsei* Ramme, 1941

(figs. 6—9, 14—15, 22, 28, pl. 1 fig. 4)

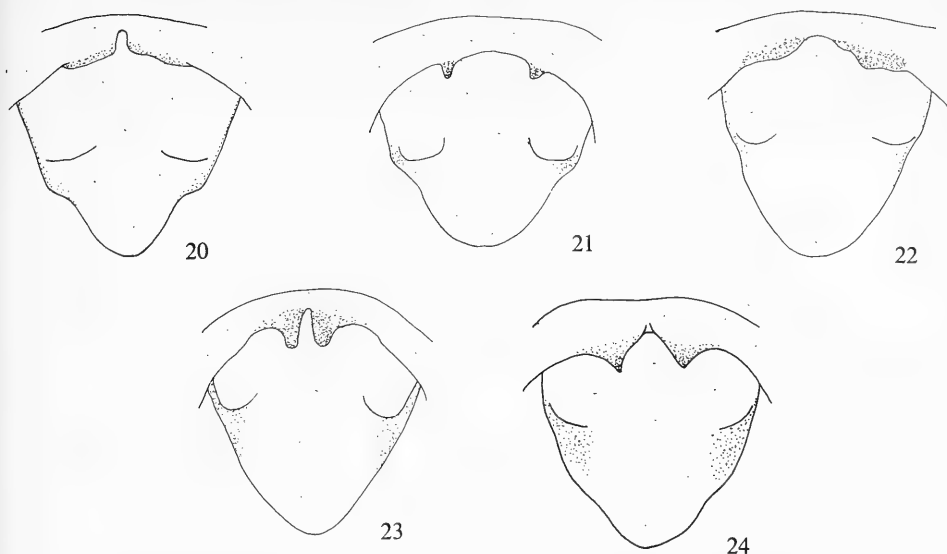
*Cranaella willemsei* Ramme, 1941: 95, 218; C. Willemse, 1956: 108, 109.

Material studied: Surigao, Philipp. 1♂ (NMM), 1♀ (ANSP) (topotypes); P.I., Dinagat, Panamana, 20.iii.1945, H. H. Roberts 1♂ (ANSP).

### Redescription.

♂, pl. 1 fig. 4. Differs from *tuberculata* as follows. Integument finely pitted, impressions weaker and smaller. Head slightly longer. Prosternal process thick, strong, roughly cubical, slightly curved anteriorly, basally slightly narrower than





Figs. 20—24. *Cranaella* species, ♂, supra-anal plate and hind margin of last abdominal tergite, dorsal view: 20, *tuberculata* Ramme, Surigao; 21, *kevani* sp.n., holotype; 22, *willemsei* Ramme, Surigao; 23, *rammei* sp.n., paratype; 24, *samarensis* sp.n., holotype.

apically, anterior side higher than posterior one, ventral side quadrate and flattened obliquely. Elytron wider, about three times as long as wide, hind margin almost straight, venation extending over a larger area. Hind wing about three quarters length of elytron, with some indistinct veins. Ridges of the fishbone pattern of the outer medial area of the hind femur prominent but without tubercles. Outer carinulae of hind femur slightly tuberculate. Hind margin of last abdominal tergite thickened, widely and weakly emarginate in the middle and with no more than an indication of a pair of furculae (fig. 22). Supra-anal plate longer than wide (fig. 22). Phallic complex as in figs. 6—9. Apex of phallus (figs. 14—15) with the ventro-posterior side slightly flattened and the tip divided into a narrow, short, medio-distal process and a stronger, auricular, lateral lobe, which is curved dorso-anteriorly.

Coloration about as in *tuberculata*, differing mainly in the ridges of the outer medial area of the hind femur which are black, sharply contrasting with the brownish colour of the hind femur.

♀. Larger than the male. Subgenital plate (fig. 28) slightly longer than wide, ventrally slightly depressed in the middle, keels moderately developed, hind margin slightly tridentate, the median point more extending posteriorly than the obtuse lateral ones. Coloration as in the male.

Measurements (length in mm): body, ♂ 25.0-26.1, ♀ 28.5-31.4; pronotum, ♂ 4.4-4.5, ♀ 5.0-5.8; elytron, ♂ 4.0-4.2, ♀ 6.4-6.7; hind femur, ♂ 12.5-13.4, ♀ 14.3-14.5.

Distribution: Philippine Is. (Mindanao; Dinagat).

Discussion. The species is well-defined by the male genitalia. The position among the other species of the genus will be discussed under *samarensis*.

***Cranaella rammei* sp.n**  
(figs. 16—17, 23, 29, pl. 1 figs. 5—6)

Material studied: ♂ holotype, ♀ allotype, 2♂ 1♀ paratypes, labelled: Dagami, Leyte, P.I., Mt. Lobi, 10 (1♂) & 21 (1♂) & 25.vi (allotype) & 4 (1♀) & 10.viii.1945 (holotype), E. R. Helwig (ANSP).

**Description.**

♂, pl. 1 fig. 5. Differing from *willemsei* as follows. General appearance more robust. Hind margin of last abdominal tergite (fig. 23) with a narrow median incision, bordered laterally by a pair of narrow, obtusely pointed furculae. Apex of phallus more elongate, distal process longer and lateral lobe moderately developed (figs. 16—17).

Coloration as in *willemsei*. Posterior veins of elytron sometimes yellowish white.

♀, pl. 1 fig. 6. Larger than the male. Subgenital plate (fig. 29) more elongate than in *willemsei*, hind margin more produced posteriorly. Coloration as in the male.

Measurements (length in mm): body, ♂ 24.2-25.1, ♀ 29.0-34.1; pronotum, ♂ 4.4-4.5, ♀ 5.8-6.0; elytron, ♂ 4.5-5.2, ♀ 5.9-6.1; hind femur, ♂ 13.3-14.2, ♀ 16.7-17.0.

Distribution: Philippine Is. (Leyte).

Discussion. The species is well-defined by the male genitalia. There are no previous records. Its position among other species will be discussed under *samarensis*.

***Cranaella samarensis* sp.n.**  
(figs. 18—19, 24, pl. 1 fig. 7)

Material studied: ♂ holotype, labelled: Island Samar, Baker (ANSP).

**Description.**

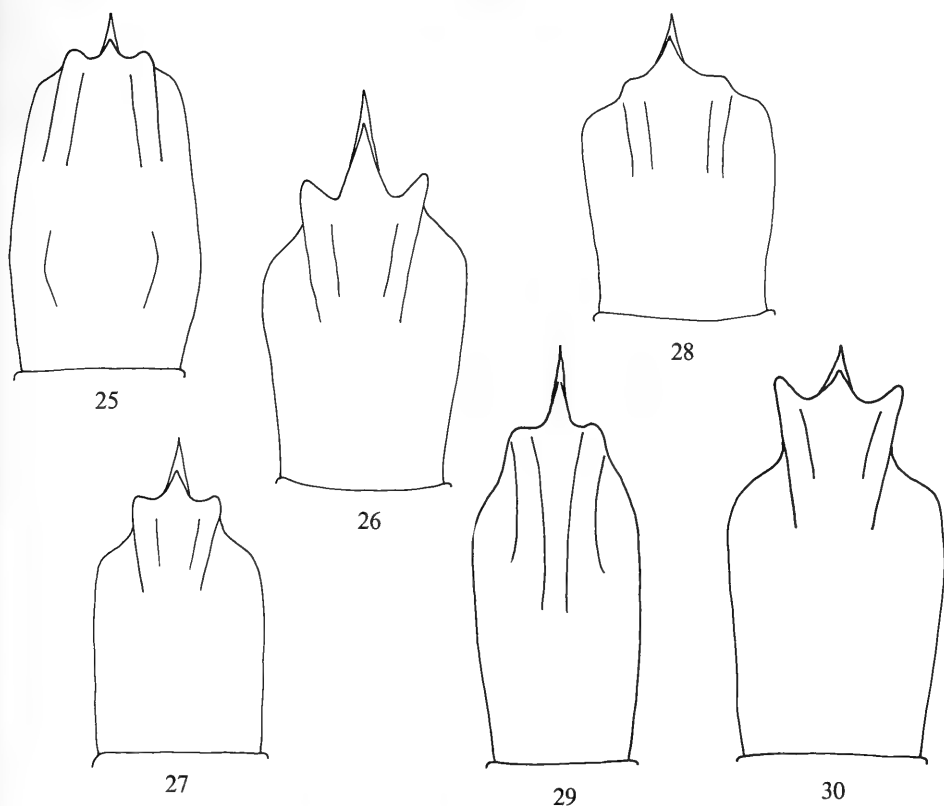
♂, pl. 1 fig. 7. Much as *willemsei*, differing in abdominal terminalia. Furculae of hind margin of last abdominal tergite large, triangular, apex pointed (fig. 24). Apex of phallus with distal process and lateral lobe intermediate between those in *willemsei* and *rammei* (figs. 18—19). Coloration as in *willemsei*.

♀. Unknown.

Measurements (length in mm): ♂, body 26.2, pronotum 4.4, elytron 4.9, hind femur 13.1.

Distribution: Philippine Is. (Samar).

Discussion. The species is defined by the furculae and the apex of phallus. Together with *willemsei* and *rammei*, the three species form a species-group characterized by the shape of the prosternal process, hind wings, apex of phallus, and



Figs. 25—30. *Cranaella* species, ♀, subgenital plate, ventral view: 25, *carnipes* Ramme, holotype; 26, *tuberculata* Ramme, Surigao; 27, *kevani* sp.n., allotype; 28, *willemsei* Ramme, topotype; 29, *rammei* sp.n., paratype; 30, *multicolor* Kevan, holotype.

black fishbone pattern of the hind femur. Both the hind wing, as well as the less pitted integument and the shape of the apex of phallus, are intermediate between the *tuberculata-kevani* group of *Cranaella* and some species of *Cranae*.

***Cranaella multicolor* Kevan, 1966**  
(fig. 30)

*Cranaella multicolor* Kevan, 1966: 41, pl. 3 figs. c—d.

This species was described after a single female from La Lun Mts., Davao Prov., Mindanao.

Marked characters may be summarized here: Pronotum with the posterior margin of the dorsum straight; posterior margin of the lateral lobe not sigmoid but straight and the lower posterior angle not produced; first transverse sulcus lacking on the dorsum and the fourth one placed more anteriorly. Prosternal process vertical and widened laterally. Elytron wide, about two-and-one-half times as long

as wide, posterior margin nearly straight, venation reaching the margins. Hind wing vestigial. Fishbone pattern of outer side of hind femur not tuberculate. Hind margin of subgenital plate strongly tridentate, the lateral points as long as and wider than the medial point (fig. 30).

Coloration. Head yellow with chocolate-brown stripe over occiput and behind eyes. Pronotum chocolate-brown. Elytron green, yellowish at base. Hind femur ochreous yellow, suffused blue-black in basal third, carinulae and fishbone pattern unicolorous. Hind knee without ante- or postgenicular rings.

Measurements (length in mm): ♀, body 28.5, pronotum 5.0, elytron 6.5, hind femur 19.5.

Distribution: Philippine Is. (Mindanao).

Discussion. The shape and venation of the elytron, the shape of the pronotum and the coloration disagree with other members of *Cranaella*. Its placement in this genus is doubtful. Pronotum and elytron agree rather with *Paracranae* C. Willemse from Celebes. However, the hind margin of the female subgenital plate and the fastigium verticis are different in that genus. A similar shape of elytron is found in *Cranae luctuosa* C. Bolívar and *Cranae kuekenthali* Brunner, both from the Moluccas. As the male of *multicolor* is unknown, a more precise allocation of the species has to be postponed.

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# A STUDY ON THE GENUS *CRANAE* STÅL (ORTHOPTERA, ACRIDOIDEA, CATANTOPINAE)

by

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With 45 text-figures and five plates

## ABSTRACT

In *Cranae* at least 20 species are recognized. Unlike in previous studies, the diagnostic emphasis is laid on morphological distinction rather than on colour characters. *Cranae rufofemorata* Willemse, and its variety *obscura*, are synonymized with *Cranae tibialis* Brunner. *Cranae patagiata coerulipes* (C. Bolívar) is considered a synonym of *Cranae patagiata* Stål. The following new species are described: *genjam*, *manokwari*, *longipennis*, *rubra* and *glabra*. Some species, preliminarily allocated to *Cranae*, link the genus along various lines with the genera *Cranaella* and *Opiptacris*.

## INTRODUCTION

*Cranae* and some related genera form a large, natural group of species, each with a very restricted range. Few characters have been used for the generic distinction. When more characters are analyzed simultaneously, the present generic classification appears largely artificial and certainly does not reflect a hypothetical phylogeny. Several species, along various lines, link the discontinuities between the genera. A generic revision is needed but material is scarce and much basic information on the species concerned is wanting. Therefore, it appears sensible to retain *Cranae* preliminarily as a taxonomic unit in its present state. Depositories of the material used in this study are given in abbreviated form throughout the text:

- |      |  |
|------|--|
| ANSP | — Academy of Natural Sciences of Philadelphia          |
| BPBM | — Bernice P. Bishop Museum, Honolulu                   |
| ITZ  | — Instituut voor Taxonomische Zoölogie, Amsterdam      |
| MC   | — Macdonald College, Quebec, Canada                    |
| MNHN | — Muséum National d'Histoire Naturelle, Paris          |
| NMM  | — Natuurhistorisch Museum, Maastricht                  |
| NMW  | — Naturhistorisches Museum, Wien                       |
| RNH  | — Rijksmuseum van Natuurlijke Historie, Leiden         |
| ZMHU | — Zoologisches Museum der Humboldt-Universität, Berlin |

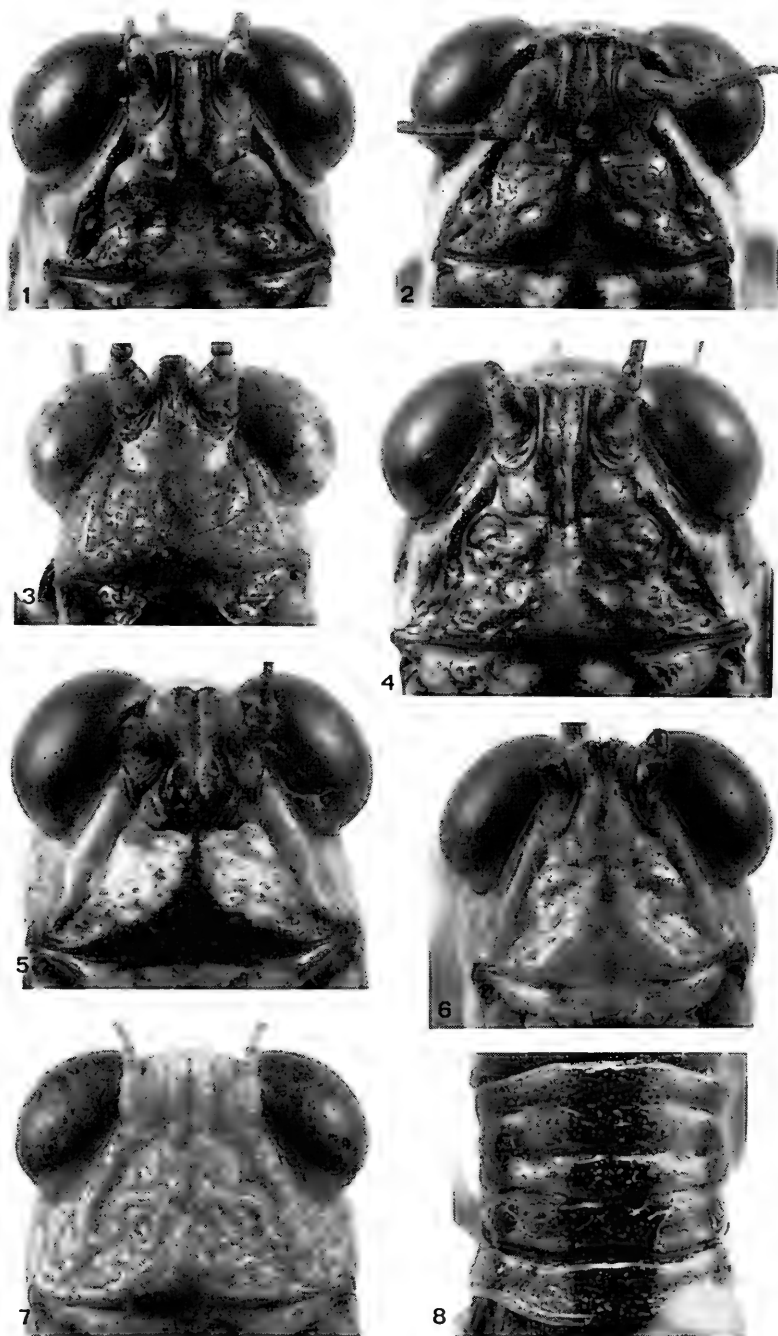


Plate 1. Figs. 1—7. *Cranae* species, face, frontal view, similar scale: 1, *patagiata* Stål, ♀ (type of *C. pervittata* Brunner); 2, *unistrigata* (De Haan) Form 1, ♀ (Aindoea R.); 3, *nigroreticulata* Brunner, ♂ (Tuguaer-Tasso); 4, *longipennis* sp.n., ♀ (allotype); 5, *luctuosa* C. Bolivar, ♀ (Telega, Obi I.); 6, *glabra* sp.n., ♀ (paratype); 7, *pictipennis* C. Willemse, ♀ (paratype). Fig. 8. *C. patagiata* Stål, ♂ (type of *C. pervittata* Brunner), pronotum, dorsal view.

My thanks are due to the following persons: J. L. Gressitt and the late Miss S. Nakata, Honolulu; M. Beier, Vienna; K. K. Günther, Berlin; P. H. van Doesburg, Leiden; M. Descamps, Paris; D. K. McE. Kevan, Macdonald College; H. Radclyffe Roberts and D. Rentz, Philadelphia; and especially to C. Jeekel, Amsterdam, for reading the manuscript and for his critical comments.

### **Cranae Stål, 1878**

*Cranae* Stål, 1878: 41, 85; Brunner, 1893: 135; 1898: 236; Kirby, 1910: 387; C. Willemse, 1921: 7, 21; C. Bolívar, 1932: 393; Uvarov, 1937: 17; C. Willemse, 1939: 74; Ramme, 1941: 87; C. Willemse, 1956: 9, 97.

Type-species: *Cranae patagiata* Stål, 1878.

A diagnosis, based on the revised material, reads as follows:

Medium size. Integument shiny. Face and pronotum more or less pitted or almost smooth, face occasionally more or less wrinkled. Occiput, on either side, with a row of slight transverse impressions.

Antennae filiform, segments up to five times as long as wide, tip reaching nearly middle of hind femur or slightly longer. Head thick, round. Eyes ovoid-hemispherical. Interocular distance as wide as or a little narrower than greatest width of fastigium verticis. Distance between eye and lower margin of cheek much shorter than vertical diameter of eye. Fastigium verticis at lower level than vertex between eyes, usually slightly marked off from rest of vertex; sometimes with fine median sulcus and fissured apex, merging with sulcus of frontal ridge; more or less widely triangular from above, truncated apex more or less wide and not reaching tip of scape; in profile, from subhorizontal to distinctly declivous, about rectangularly meeting face. Face (pl. 1 figs. 1—7) slightly reclinate. Frontal ridge present only above the median ocellus, weakly sulcate; margins obtuse, nearly parallel, sometimes connected transversely at median ocellus. Lateral facial keels straight, low, more or less divergent; face, along these keels, depressed in some species. Occiput and cheeks convex.

Pronotum (pl. 1 fig. 8, pl. 2 fig. 9—16) about as long and as wide as head or slightly shorter or narrower, without keels, cylindrical or dorsum slightly depressed from above, lateral lobes parallel or slightly compressed laterally in the middle. Four transverse sulci, more or less deep, second one dorsally only. Dorsum divided by the sulci into five parts; width of these parts varying individually, but distance between second and third sulci usually slightly smaller, that between third and fourth sulci usually slightly larger. Lateral lobe about as long as high or shorter; deepest point at level of third sulcus, from there lower margin concave anteriorly, straight or slightly convex posteriorly; anterior angle obtuse-angulate, posterior angle about rectangular, from narrowly rounded to obtusely pointed. Anterior margin of dorsum weakly rounded, of lateral lobe straight and divergent anteriorly. Posterior margin of dorsum weakly rounded, straight or weakly emarginate, of lateral lobe straight or slightly concave, vertical or slightly slanting upwards posteriorly. Prosternal process strong, more or less

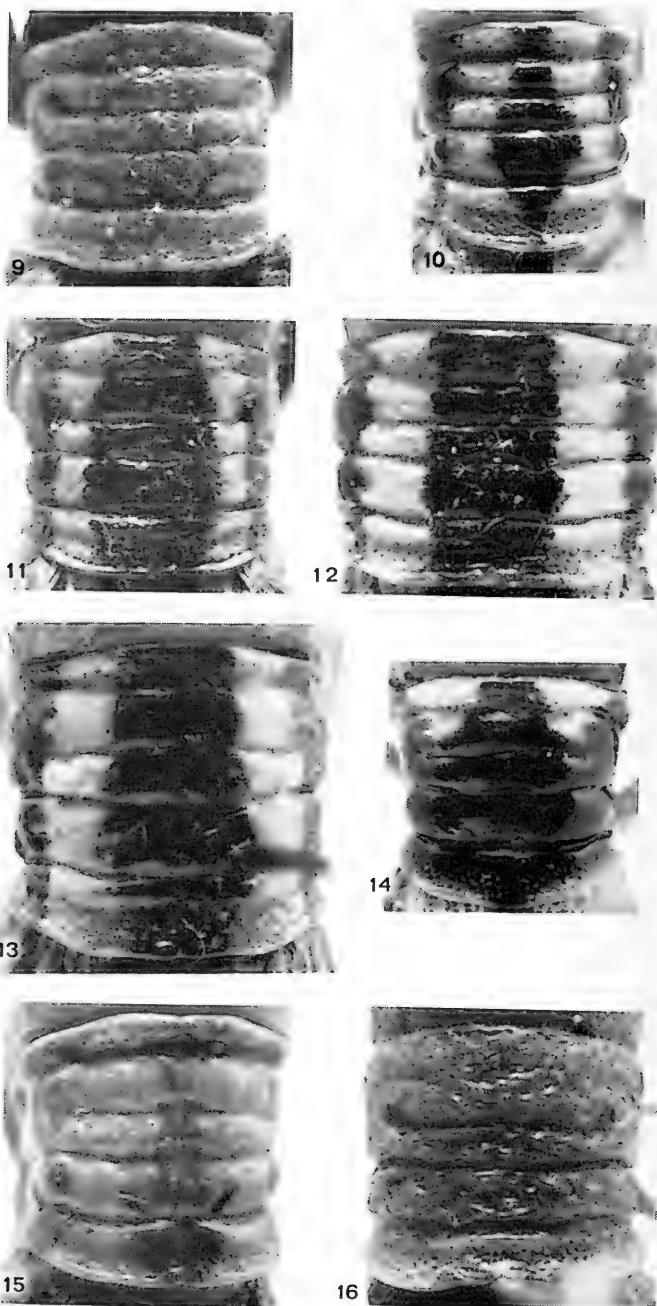


Plate 2. Figs. 9—16. *Craneae* species, pronotum, dorsal view, similar scale: 9, *tibialis* Brunner, ♂ (holotype); 10, *nigroreticulata* Brunner, ♂ (Tuguaer-Tasao); 11, *unistrigata* (De Haan), Form 1, ♂ (Fak Fak, T.C. Maa); 12, *trivittata* C. Willemse, ♀ (Bivak Eiland); 13, *rufipes* Ramme, ♀ (Finschhafen); 14, *luctuosa* C. Bolivar, ♂ (Telaga, Obi I.); 15, *glabra* sp.n., ♀ (paratype); 16, *pictipennis* C. Willemse, ♂ (allotype).



laterally compressed, in profile vertical or slightly directed anteriorly; truncated apex widened laterally, its anterior margin straight and posterior margin curved towards anterior one. Mesosternal lobes wider than long, inner margins convex, interspace wider than long, about as wide as a lobe. Metasternal interspace narrowly triangular. Mesonotum about two-thirds of metanotal length. Metanotum narrower than distance between anterior margin of pronotum and second pronotal sulcus.

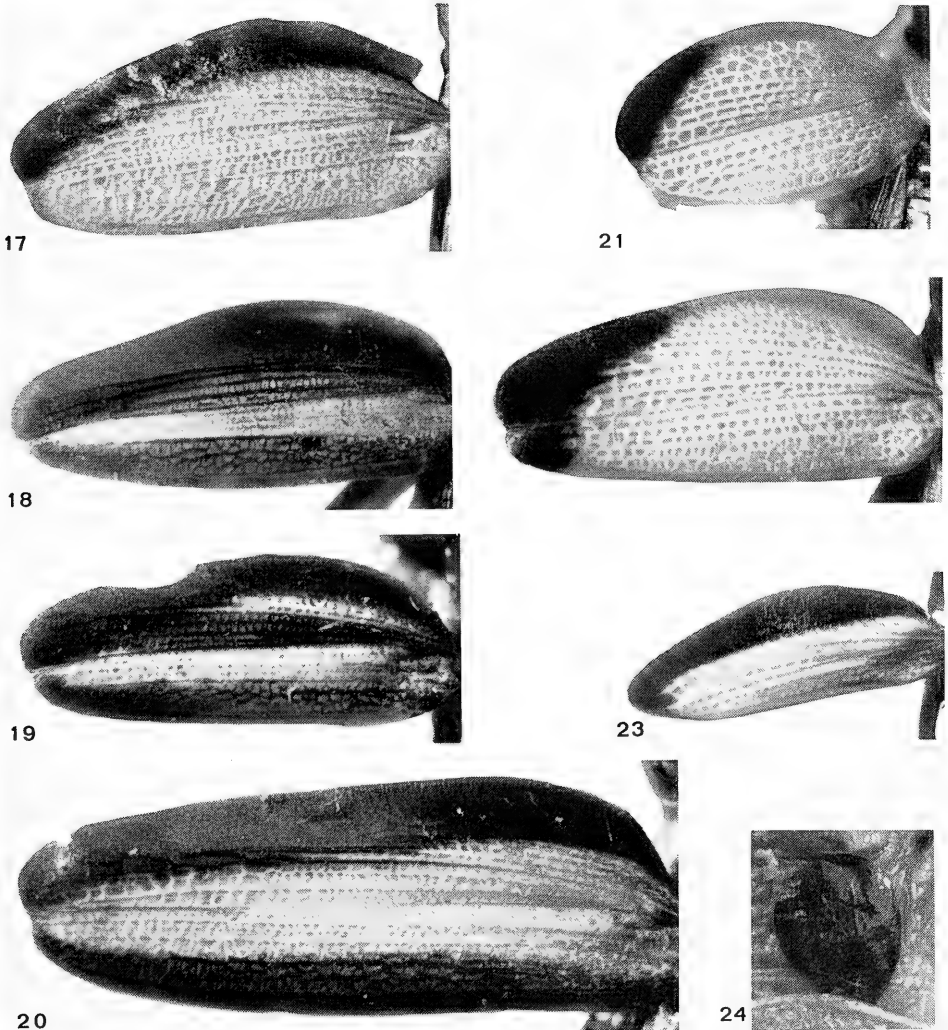


Plate 3. Figs. 17—24. *Cranae* species, spread left elytron, outer view, similar scale: 17, *patagiata* Stål, ♀ ('Java'); 18, *unistrigata* (De Haan), Form 1, ♀ (Aindoea R.); 19, *manokwari* sp.n., ♀ (allotype); 20, *longipennis* sp.n., ♀ (allotype); 21, *kuekenthali* Brunner, ♀ (Halmaheira, T. Barbour); 22, *luctuosa* C. Bolívar, ♀ (Telaga, Obi I.); 23, *glabra* sp.n. ♀ (paratype); 24, *pictipennis* C. Willemse, ♀ (holotype) (in situ)

Tegmina (pl. 3 fig. 17—24) from squamipterous to subbrachypterous, ranging from reaching first up to ninth abdominal tergite. Elytra touching each other or more or less separated dorsally; from almost as long as wide to three times as long as wide; posterior margin from straight to strongly rounded; anterior margin more or less evenly rounded or tapering in apical half; apex, at the end of folding of elytron, divided into a larger anterior and a smaller posterior lobe (except *glabra* and *pictipennis*); venation simple, a wider zone along the anterior and a much narrower one along posterior margin without veins. Hind wing slightly shorter than elytron, with sparse veins (as a small, membranous fold in *pictipennis*). Tympanum open, almost circular, level with the body surface (as a closed, narrow furrow in *pictipennis*).

Legs stout (attenuate in *glabra*). Hind femur about reaching tip of abdomen (male), or slightly shorter (female); fishbone pattern distinct and smooth, keels smooth or slightly crenulate, inner lower carinula pilose. Knee-lobes truncate. Brunner's organ present. Hind tibia slightly shorter than hind femur; margins rounded, strongly pilose; six or seven inner and four or five outer spines regularly arranged, apical ones included. Hind tarsus pilose, slightly longer than half the tibial length, third segment longest, first and second segments of about equal length.

Male. — Hind margin of last abdominal tergite (fig. 5) triangularly excised with a pair of well-separated, small, widely triangular furculae. Supra-anal plate (fig. 5) wider than long, roughly triangular; lateral margins thickened near base and there with a short, low, transverse ridge, extending medially; middle of basal half depressed; apex more or less widely parabolic. Cercus slender, slightly up- and incurved, pointed apex reaching or extending beyond tip of subgenital plate. The latter subconical, short and its apex obtuse.

Phallic complex, figs. 6—45. Epiphallus narrowly bridge-shaped; ancorae, in most species, more (fig. 7) or less (fig. 14) joined with lateral plates, in few species present as a separate projection (fig. 11); inner lophi smaller and tooth-shaped, outer lophi larger and hook-shaped. Ectophallic membrane with shield-shaped dorsal sclerite. Cingulum with narrowly U-shaped apodemal structure. Rami extending latero-ventrally and dorso-posteriorly; usually narrow (fig. 9), but in some species wider (fig. 13). Cingular valves short, not by far reaching tip of apical penis valves, triangular from above. Apical penis valves slightly upcurved and joining laterally with sheath of penis. Apex of phallus formed by sheath of penis and projecting ends of apical penis valves. Shape of apex of phallus variable but species-specific (figs. 16—45).

Female. — Hind margin of last abdominal tergite triangularly excised. Supra-anal plate tongue-like, twice as long as wide, apex parabolic. Cercus conical, slightly outcurved, not reaching tip of supra-anal plate. Subgenital plate (fig. 1) twice as long as wide, ventral surface flattened in the middle and, usually, rather depressed or sulcated apically between a pair of short, obtuse, longitudinal keels; hind margin slightly sigmoid laterally, tridentate in the middle, median point longest and widest, lateral points corresponding with distal ends of ventral keels. Dorsal aspect of subgenital plate (fig. 3) with a pair of simple, round columellae.

Valves of ovipositor (fig. 2) slender, straight, margins finely serrate or almost smooth, apices not definitely hooked. Lateral basivalvular sclerite elongate-triangular, ventral basivalvular sclerite three to four times as long as wide. Spermatheca (fig. 4) simple, with an apical diverticulum and a wider, strongly curved, preapical diverticulum.

Coloration. Most species characteristically coloured. Sexual dichromatism not apparent. Individual variation appearing to be slight, but a general statement not possible by lack of material. Coloration of the following parts similar in all taxa of the genus: eyes, individually, from yellow to dark brown; apical part of mandible black; crescents of hind knee dark castaneous brown; spines of hind tibia and claws of tarsus dark brown or blackish, tips black; furculae in the male black.

General distribution: New Guinea and the Moluccas.

Discussion. Previously, ten species and three subspecies have been placed in *Cranae* (C. Willemse, 1956). Now at least 20 species are recognized. *Opiptacris pictipennis* (C. Willemse) has been re-established to its original combination *Cranae pictipennis* (F. Willemse, 1975: 121). *Cranae rufofemorata* C. Willemse and its variety *obscura* are both considered conspecific with *Cranae tibialis* Brunner. *Cranae patagiata coerulipes* (C. Bolivar) is considered conspecific with *Cranae patagiata* Stål. The available material clearly shows that *Cranae unistrigata* (De Haan) and *trivittata* C. Willemse belong to a complex of closely related populations. Two of these have been described by Ramme, as *caprai* and *trivittata rufipes*, respectively. Whether *caprai* should be considered taxonomically distinct from nominate *unistrigata* is an open question. However, *rufipes* is now given specific rank. As to the remaining material resembling nominate *unistrigata* and *trivittata*, it is still hard to decide whether speciation has been completed or not. In two cases only differences seem sufficient for distinction on species level: *genjam* and *manokwari*. Eight additional species are recognized as new. Three are fully described and named: *longipennis*, *rubra* and *glabra*. The others could not be defined precisely enough, by lack of males. They are briefly recorded, but not yet named.

In *Cranae*, some natural species groups can be distinguished. The main stock of the genus is found on New Guinea. It is formed by the *unistrigata* complex. The following groups among *Cranae* may be recognized: (1) nominate *unistrigata*, *genjam*, and (probably) the not fully known species from Roon I. and Sabang; (2) *trivittata*, *rufipes*, *manokwari* and (probably) the not fully known species from Buba and Normanby I.; (3) *rubra*; (4) *longipennis* and (probably) the not fully known species from Aseki; (5) *patagiata*, *tibialis*; (6) *nigroreticulata*; (7) species with important discontinuity as *kuekenthami*, *luctuosa*, *glabra*, and *pictipennis*. Especially the latter group of species links, through various characters, *Cranae* with *Cranaella* Ramme and *Opiptacris* Walker.

Key to the species of *Cranae* (*emendata* Brunner and the now recognized but not yet named new species omitted):

1. Elytron circular and not reaching beyond the first abdominal tergite (pl. 3 fig. 24); tympanum closed (Buru) . . . . . *pictipennis* C. Willemse (p. 149)

- Elytron elongate and reaching beyond the first abdominal tergite (pl. 3 figs. 17—23); tympanum open, circular . . . . . 2
- 2. Elytron unicolorous olivaceous green, without black (Kei Is.) . . . . . *tibialis* Brunner (p. 132)
- Elytron with at least the anterior margin and the apex bordered with black or dark brown . . . . . 3
- 3. Elytron red and black . . . . . 4
- Elytron without red . . . . . 5
- 4. Hind femur red on basal half (Woodlark I) . . . . . *rubra* sp.n. (p. 144)
- Hind femur not red (Ambon; Ceram) . . . . . *patagiata* Stål (p. 128)
- 5. Elytron not reaching beyond the second abdominal tergite (pl. 3 fig. 23) (Biak I.) . . . . . *glabra* sp.n. (p. 147)
- Elytron longer (pl. 3 fig. 17—22) . . . . . 6
- 6. Pronotum cylindrical, without longitudinal fasciae (pl. 2 fig. 14); phallic complex with the rami wide (fig. 13) . . . . . 7
- Pronotum slightly depressed from above, with longitudinal fasciae (pl. 2 figs. 10—13); phallic complex with the rami narrow (fig. 9) . . . . . 8
- 7. Hind femur orange on basal half (Halmahera) . . . . . *kuekenthali* Brunner (p. 145)
- Hind femur not orange on basal half (Obi I.) . . . . . *luctuosa* C. Bolívar (p. 146)
- 8. Median black fascia of pronotal dorsum rhomboidally widened in the middle (pl. 2 fig. 10) (Halmaheira) . . . . . *nigroreticulata* Brunner (p. 135)
- This fascia not widened in the middle (pl. 2 figs. 11—13) . . . . . 9
- 9. Elytron wide and long, margins about parallel, the yellow streak wide (pl. 3 fig. 20) (S. New Guinea) . . . . . *longipennis* sp.n. (p. 142)
- Elytron shorter, tapering apically, the yellow streak narrow (pl. 3 figs. 18—19) . . . . . 10
- 10. Yellow antegenicular ring of hind femur bordered proximally with red or orange . . . . . 11
- This ring bordered proximally with a narrow black ring, either complete or not . . . . . 12
- 11. Apex of phallus short (figs. 22—23) (Genjam, near Hollandia) . . . . . *genjam* sp.n. (p. 140)
- Apex of phallus elongate (figs. 24—31) (W & N. New Guinea) . . . . . *unistrigata* De Haan (p. 135)
- 12. Pronotum shorter, dorsum more depressed (pl. 2 fig. 12); head more globose (SW. New Guinea) . . . . . *trivittata* C. Willemse (p. 140)
- Pronotum longer, dorsum less depressed (pl. 2 fig. 13); head less globose (N. New Guinea) . . . . . *rufipes* Ramme (p. 141) and *manokwari* sp.n. (p. 142)

### ***Cranae patagiata* Stål, 1878**

(figs. 1—2, 5—10, 16—17, pl. 1 figs. 1, 8, pl. 3 fig. 17, pl. 4 fig. 25)

*Cranae patagiata* Stål, 1878: 85; Brunner, 1898: 236; Kirby, 1910: 387; Sjöstedt, 1932: 62; C. Willemse, 1939: 74; Ramme, 1941: 87, 88; C. Willemse, 1956: 104 (not Brit. N. Guinea).

*Cranae patagiata patagiata*; C. Willemse, 1956: 99.

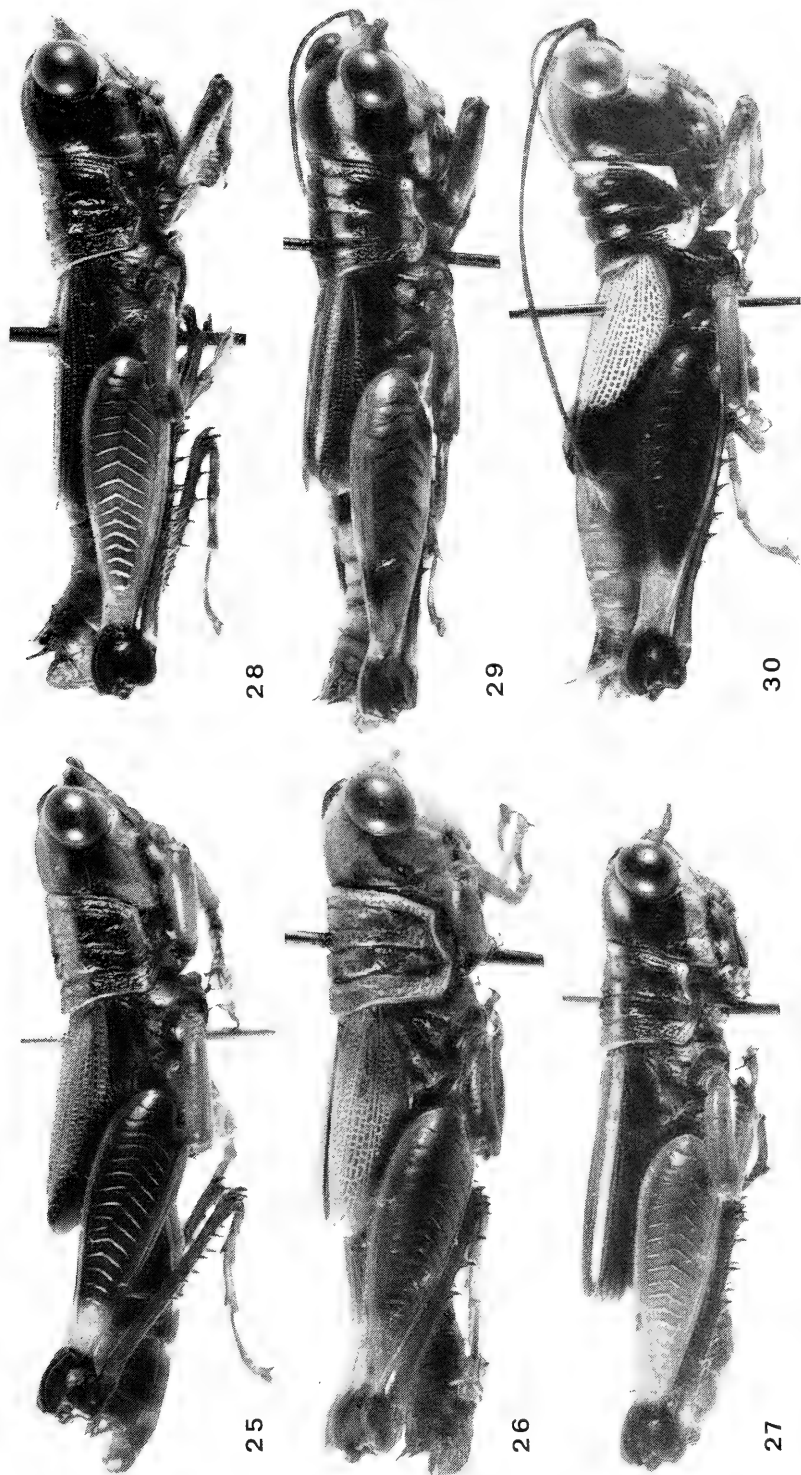


Plate 4. Figs. 25—30. *Cranae* species, lateral view: 25, *patagiata* Stål, ♂ (type of *C. pervittata* Brunner); 26, *tibialis* Brunner, ♂ (paratype of *C. rufofemorata* C. Willemse); 27, *unistrigata* (De Haan), ♂ (holotype); 28, *genjam* sp.n., ♂ (holotype); 29, *manokwari* sp.n., ♂ (holotype); 30. *luctuosa* C. Bolívar, ♂ (Telaga, Obi I.).

*Cranae pervittata* Brunner, 1898: 236, 238; Kirby, 1910: 387; C. Willemse, 1922: 716; C. Bolívar, 1923: 146; C. Willemse, 1939: 74; Ramme, 1941: 88 (synonymy established); C. Willemse, 1956: 104 (in synonymy only).

*Cranae pervittata pervittata*; C. Bolívar, 1923: 147; C. Willemse, 1939: 74.

*Cranae pervittata coerulipes* C. Bolívar, 1923: 147; C. Willemse, 1939: 74. **Syn. nov.**

*Cranae patagiata coerulipes*: Ramme, 1941: 88 (nec *coerulescens*); C. Willemse, 1956: 99, 105; Kevan, 1966: 411.

Material studied: ♂ lectotype, ♀ paralectotype of *Cranae patagiata*, labelled: Col. Br. v. W. Amboina, 1258, det. Br. v. W. *Cranae patagiata* (NMW). Both specimens discoloured.

Types of *Cranae pervittata*, 1♂ 1♀, labelled: Coll. Br. v. W. Amboina Staudinger, 14.141, Det. Br. v. W. *Cranae pervittata*, Type, *Cranae patagiata* Stål Ramme det. 1939 (NMW).

Additional material: Amboina, Dr. Doleschal, 1859 (2♂, 2♀, discoloured) (NMW); Molukken, Depuiset ded., 5043, det. Br. v. W., *Cranae pervittata* (1♀) (NMW); Amboine, Moluques, Collection Brunner, *Cranae patagiata* Stål, collection A. Finot (1♂, 1♀, discoloured) (MNHN); Amboine, Collection A. Finot, *Cranae pervittata* Br. (1♂) (MNHN); Ceram, Piroe (1♂) (ZMHU); Ceram, Piru, F. Barbour, 1906-07 coll. (1♀, discoloured) (ANSP); Java, Oberth., ex coll. Bolívar, *Cranae patagiata*, det. C. Willemse (1♀) (NMM).

### Redescription.

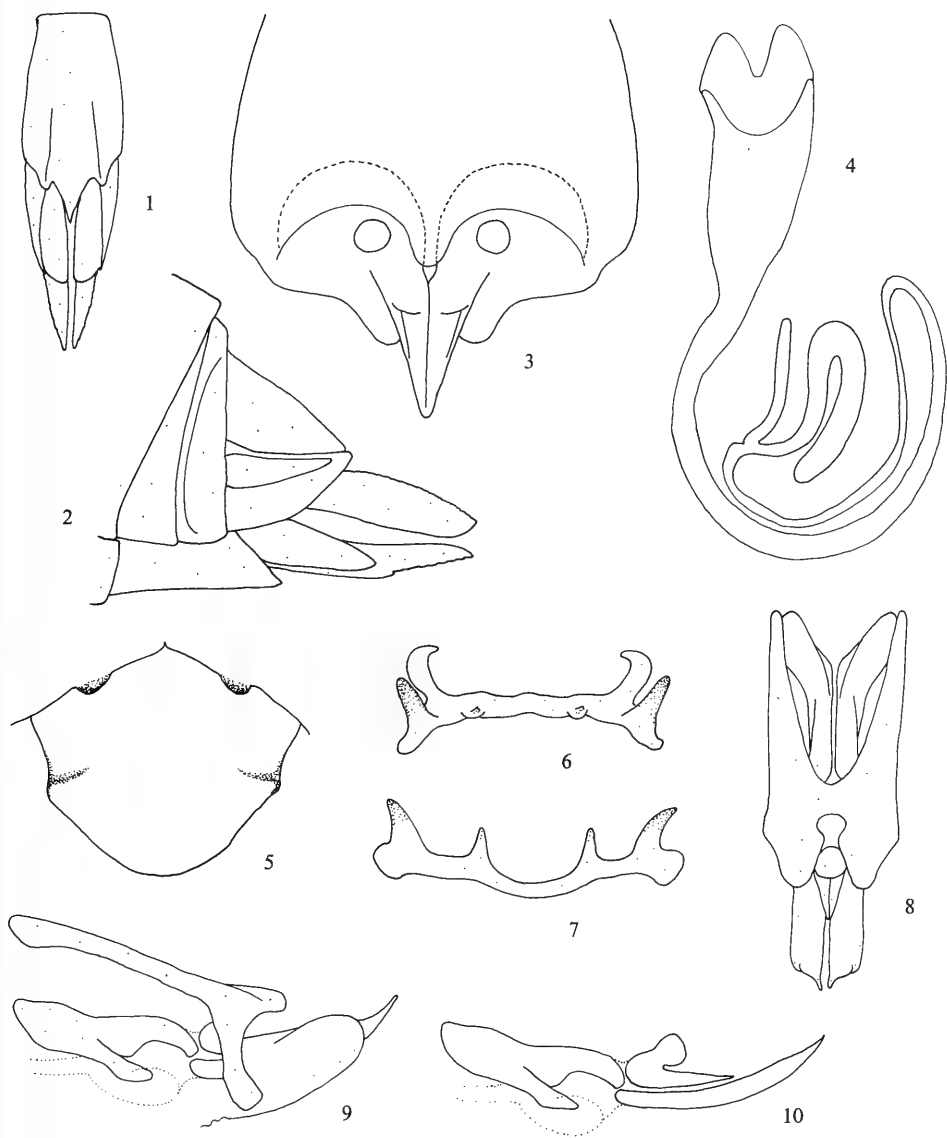
Male, pl. 4 fig. 25. Face and thorax slightly pitted. Interocular distance less than greatest width of fastigium verticis. Fastigium verticis triangular, greatest width and length about equal, finely sulcate apically, in profile slightly declivous. Frontal ridge with low margins, below median ocellus disappearing into slightly wrinkled surface of face. Face slightly transversely convex, weakly impressed along lateral keels.

Pronotum (pl. 1 fig. 8) as long and as wide as head, slightly depressed from above, lateral lobe parallel; sulci moderate; posterior margin of dorsum slightly extending posteriorly, straight or very slightly rounded; lateral lobe as long as high, posterior angle narrowly rounded, posterior margin straight and vertical.

Elytron reaching middle of hind femur, about three times as long as wide, posterior margin straight, anterior margin strongly rounded basally, tapering apically towards the widely rounded, divided apex. Both elytra touching each other apically, narrowly separated basally.

Supra-anal plate (fig. 5) with the apex widely parabolic. Furculae (fig. 5) very small, well separated. Cerci reaching tip of subgenital plate. Phallic complex, figs. 6—10, 16—17. Ancorae of epiphallus joined with lateral plates. Cingular rami narrow. Apex of phallus with moderately developed sheath of penis and short, strongly tapering apical penis valves, their tips almost pointed.

Coloration olivaceous yellow, dark bluish-black and red. Antennae dark brown, paler apically. Head and pronotum olivaceous yellow with three bluish-black fasciae: on either side, from behind eye over middle part of pronotal lateral lobe and a median fascia from between the eyes over occiput and pronotal dorsum; margins of fastigium verticis and frontal ridge, lateral facial keels and larger or



Figs. 1—2. *Cranae patagiata* Stål, ♀ (type of *C. pervittata* Brunner): 1, tip of abdomen, ventral view; 2, same, lateral view. Figs. 3—4. *Cranae unistrigata* (De Haan), Form 6, ♀ (Hollandia): 3, subgenital plate, dorsal view; 4, spermatheca. Figs. 5—10. *Cranae patagiata* Stål, ♂ (type of *C. pervittata* Brunner): 5, furculae and supra-anal plate; 6, epiphallus, dorsal view; 7, same, posterior view; 8, phallic complex, dorsal view, epiphallus and part of ectophallic membrane removed; 9, same, lateral view; 10, same, endophallus.

smaller areas of face, bluish or greenish-black; episternum, meso- and metathorax blackish, except for yellowish lower part of second episternum and epimerum.

Elytron dull red, anterior margin and apex widely bordered with black. Hind wing infumate. Abdomen violaceous brown and yellowish. Fore and middle femora dull red, apical margins of knees, whole tibiae and tarsi olivaceous green and yellow. Hind femur ranging from violaceous black to yellowish; in the former case, dorsal side yellowish, in the latter one, carinulae and fishbone pattern black. Antegenicular part of hind femur, as long as length of hind knee, yellow. Hind knee, tibia and tarsus dark bluish-green; hind tibia with a narrow, indistinct, greenish postgenicular ring; hind tarsus paler below.

Female. Larger than male. Face, pl. 1 fig. 1. Elytra (pl. 3 fig. 17) more widely separated dorsally and reaching distal end of basal third of hind femur, about two-and-one-half times as long as wide. Abdominal terminalia, figs. 1—2. Subgenital plate distinctly sulcate apically. Coloration as in male.

Measurements (length in mm): body, ♂ 22.0–23.0 ♀ 27.0–30.0; pronotum, ♂ 4.2–4.5, ♀ 5.2–5.8; elytron, ♂ 8.2–8.8, ♀ 7.6–8.9; hind femur, ♂ 11.7–12.2, ♀ 13.6–14.9.

Distribution: Moluccas (Ambon, Ceram).

Discussion. The species is well-defined, especially by the phallic complex and the coloration. The apex of phallus comes close to that of *tibialis* and *genjam*. The coloration of the elytron is much as in *rubra*.

The discoloured pair, bearing Brunner's identification label *patagiata*, lacks any type indication. In agreement with the original paper, the record by Sjöstedt (1932) and Ramme's opinion (1941), the pair should be considered Stål's types. The male is hereby designated **lectotype**. Ramme synonymized Brunner's *pervittata* with Stål's *patagiata*. Comparison of the phallic complex definitely reveals their synonymy. Bolívar's *pervittata coerulipes* from Ceram is defined by slightly distinct coloration. However, this character is not reliable as among *patagiata* material from Ambon (MNHN) a transitional form is also found. Besides, genitalia and other characters are very similar and the localities quite close. Bolívar's *coerulipes* is considered conspecific with *patagiata*.

The previous records from British New Guinea (material not at hand) and Java (1 ♀ at hand) are probably incorrect. As to the former, see below under *rubra*.

### ***Cranae tibialis* Brunner, 1898** (figs. 18—19, pl. 2 fig. 9, pl. 4 fig. 26)

*Cranae tibialis* Brunner, 1898: 236, 237; Kirby, 1910: 287; C. Willemse, 1939: 74; 1956: 98, 99.

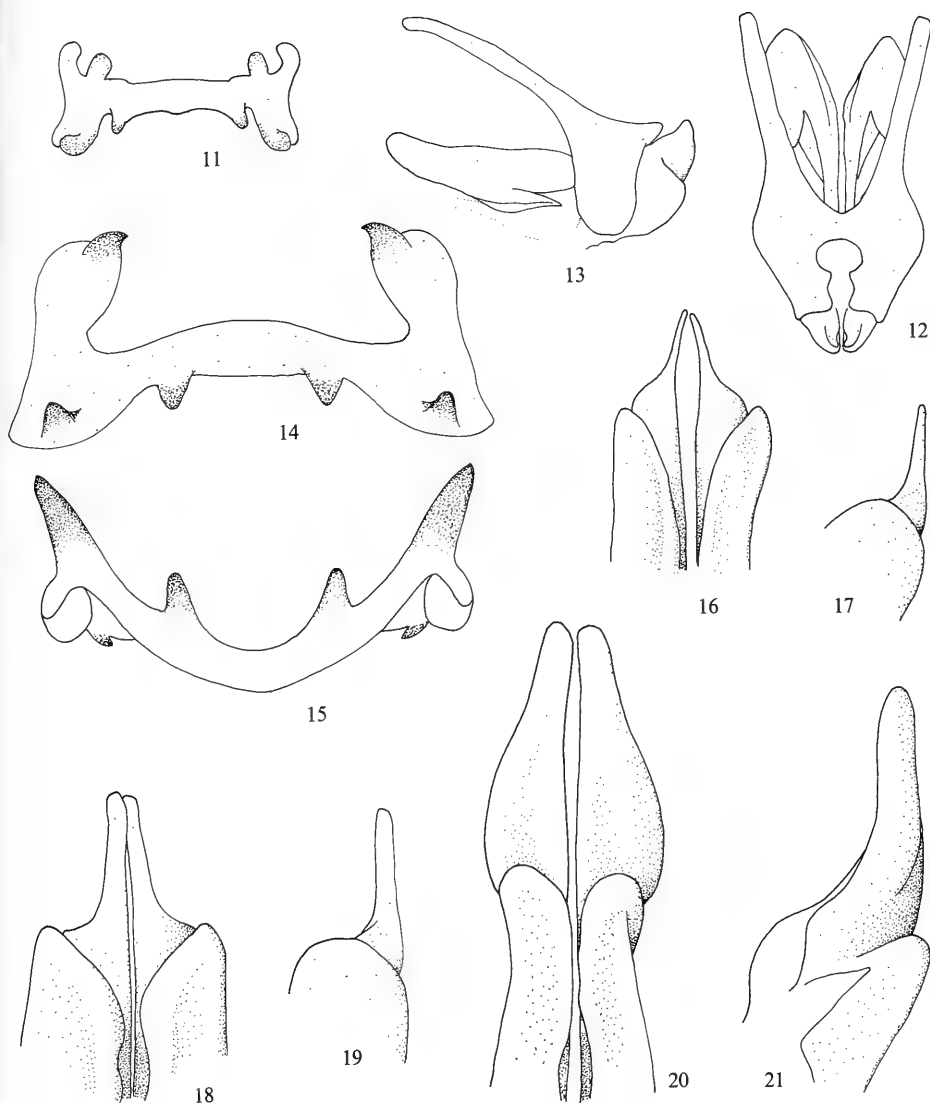
*Cranae rufofemorata* C. Willemse, 1939: 73, 74, fig. 1; 1956: 98, 100, fig.: F. Willemse, 1966a: 38; 1966b: 65. **Syn. nov.**

*Cranae rufofemorata* var. *obscura* C. Willemse, 1956: 98, 101; F. Willemse, 1966a: 38; 1966b: 65. **Syn. nov.**

Material studied: ♂ holotype of *Cranae tibialis*, labelled: Coll. Br. v. W. Key-Inseln Ribbe leg., det. Br. v. W. *Cranae tibialis*, Type (NMW). The specimen lacks both antennae; right tegmina are spread.

Type-series of *Cranae rufofemorata*, labelled: H. C. Siebers Kei Eil., Gn. Daab





Figs. 11—13. *Cranae kuekenthali* Brunner, ♂ (paratype): 11, epiphallus, dorsal view; 12, phallic complex, dorsal view, epiphallus and part of ectophallic membrane removed; 13, same, lateral view. Figs. 14—15. *Cranae longipennis* sp.n., ♂ (holotype): 14, epiphallus, dorsal view; 15, same, posterior view. Figs. 16—21. *Cranae* species, ♂, tips of apical penis valves and sheath of penis, ventro—posterior (even numbers) and left lateral (odd numbers) view, similar scales: 16—17, *patagiata* Stål (type of *C. pervittata* Brunner); 18—19, *tibialis* Brunner (paratype of *C. rufofemorata* C. Willemse); 20—21, *nigroreticulata* Brunner (Tuguaer—Tasao).

143 (♂ holotype) & 138 (1♂ paratype) & Toetal 201 (1♂ paratype, ♀ allotype), *Cranae rufofemorata* n.sp. C. Willemse det. (Holo- and allotype RNH, paratypes NMM). The holotype lacks both antennae.

Type-series of *Cranae rufofemorata* var. *obscura*, labelled: H. C. Siebers Kei Eil. Gn. Daab 85 (♀ holotype) & 135 (♀ paratype), *Cranae rufofemorata* Will. var. *obscura* n.var. Det. C. Willemse (NMM). The holotype lacks the right antenna and both fore legs.

### Redescription

Male, pl. 4 fig. 26. Differs from type-species in pronotum, apex of phallus and coloration. Pronotum (pl. 2 fig. 9) more cylindrical, slightly wider, sulci slightly deeper, posterior margin extending less posteriorly and lateral lobe narrower. Apex of phallus (figs. 18—19) slightly larger, sheath of penis more developed, apical penis valves more narrowing apically and tips larger.

Coloration as described by C. Willemse (1956) under *rufofemorata* and its variety *obscura*. Marked characters may be summarized as follows: head from yellowish or yellowish-green to almost completely dark olivaceous; pronotum from yellowish-brown to blackish-brown, in the latter case with the margins yellowish-brown; elytron completely yellowish or greenish; legs red, except for hazel brown hind knees with blackish lobes, a yellowish-green antegenicular ring of hind femur, dark brownish or violaceous apical third of hind tibia, and brownish or greenish tarsi.

Female. Larger than male. Abdominal terminalia as in type-species. Coloration as in male, except for hind femur, which is yellowish-green with lower inner marginal area red.

Measurements (length in mm): body, ♂ 21.0—22.0, ♀ 31.0—35.0; pronotum, ♂ 4.0—4.3, ♀ 5.2—5.4; elytron, ♂ 7.7—8.0, ♀ 7.5—8.2; hind femur, ♂ 11.3—12.5, ♀ 14.2—15.2.

Distribution: Moluccas (Kei Is.).

Discussion: The species is well-defined, especially by the apex of phallus and the coloration. Apex of phallus much as in *patagiata* and *genjam*. The unicolorous elytra without black forming a particular feature of the species. Shape and coloration of the pronotum intermediate between *patagiata* and the *kuekenthaliluctuosa* group.

As against the original statement and in agreement with the given measurements, the holotype is not a female but a male. Comparison of the holotype of *tibialis* with the males of the type-series of *rufofemorata*, clearly reveals their synonymy. C. Willemse distinguished among *rufofemorata*, the variety *obscura*. It was based on the dark olivaceous green head and pronotum in two females of the type-series of *rufofemorata*. However, this character is not reliable, as the colour of head and pronotum in males of nominate *rufofemorata* ranges from pale olivaceous green to as dark as in *obscura*. The darkest male of nominate *rufofemorata* is the holotype (RNH). C. Willemse's distinction may be explained by assuming that this holotype was not before him when he described the variety (1956). By lack of distinct features, I consider *obscura* conspecific with *rufofemorata* as well as with *tibialis*.

***Cranae nigroreticulata* Brunner, 1898**

(figs. 20—21, pl. 1 fig. 3, pl. 2 fig. 10)

*Cranae nigroreticulata* Brunner, 1898: 198, 236, 239; Kirby, 1910: 387; C. Willemse, 1922: 715; 1939: 74; Ramme, 1941: 90; C. Willemse, 1956: 98, 101.

*Cranae marginata* Brunner, 1898: 198, 236, 237 (partim); Kirby, 1910: 387 (do); Ramme, 1941: 87, 90 (♀ synonymy established); C. Willemse, 1956: 101 (in synonymy only).

Material studied: 1 ♂, labelled: Halmahera, Tuguaer-Tasoa, 100-150 m, 20 ix. 1951 (1 ♂) (NMM).

**Redescription**

Male. Differs from the type-species in head, pronotum, abdominal terminalia, and coloration. Fastigium verticis narrowly triangular, apex not fissured, in profile subhorizontal. Face (pl. 1 fig. 3) more pitted, not wrinkled, more transversely convex, lateral keels lower. Frontal ridge weaker. Pronotum (pl. 2 fig. 10) narrower, sulci slightly wider and posterior margin of lateral lobe slightly concave.

Furculae larger, more pointed and closer together. Supra-anal plate shorter, apex wider and transverse ridges more distinct. Apex of phallus larger and more elongate (figs. 20—21); sheath of penis narrow; apical penis valves wider and less tapering apically.

Coloration as described by C. Willemse (1956). Marked characters may be summarized as follows: head yellow; pronotum orange-yellow, dorsum with a black median fascia, in the middle rhomboidally widened, lateral lobe with a black fascia in upper part; elytron yellowish, anterior margin narrowly, apex widely bordered with black; fore and middle legs orange-yellow with some black markings; hind femur orange-yellow with carinae, carinulae and fishbone pattern black, antegenicular area completely orange-yellow; hind knee black; hind tibia and tarsus violaceous black.

Female. Not studied.

Measurements were given in previous papers.

Distribution: Moluccas (Halmahera).

Discussion. The species is well-defined by the face, apex of phallus and coloration. The pitted and not wrinkled face and the rhomboidal figure of the pronotal dorsum are unique in *Cranae*. The apex of phallus agrees with *unistrigata* rather than with *patagiata*.

Type-material of *Cranae marginata* was not at hand. No comments are given as to the synonymic notes in Ramme (1941).

***Cranae unistrigata* (De Haan, 1842)**

(figs. 3—4, 24—31, pl. 1 fig. 2, pl. 2 fig. 11, pl. 3 fig. 18, pl. 4 fig. 27)

*Acridium (Oxya) unistrigatum* De Haan, 1842: 143, 156, 158, 246, pl. 21 figs. 7—7a (♂), 8 (juv. ♂, not ♀);

I. Bolívar, 1918: 42 (juv. ♂, not ♀); C. Willemse, 1928: 11.

*Acridium unistrigatum*; Stål, 1873: 53.

*Oxya unistrigata*; Walker, 1870: 648.

*Oxya (?) unistrigata*; Kirby, 1910: 395 (juv. ♂, not ♀).

*Taeniophora unistrigata*; Bruner, 1907: 245, 247.

*Chitaura haani* I. Bolívar, 1918: 34 (juv. ♂, not ♀); C. Willemse, 1956: 106 (in synonymy only).

*Cranæ unistrigata*; I. Bolívar, 1898: 88; Kirby, 1910: 387; C. Willemse, 1922: 716; 1932: 46; 1939: 75; Ramme, 1941: 87, 90; C. Willemse, 1956: 99, 106 (not Sabang); Kevan, 1966: 411 (not Roon I).

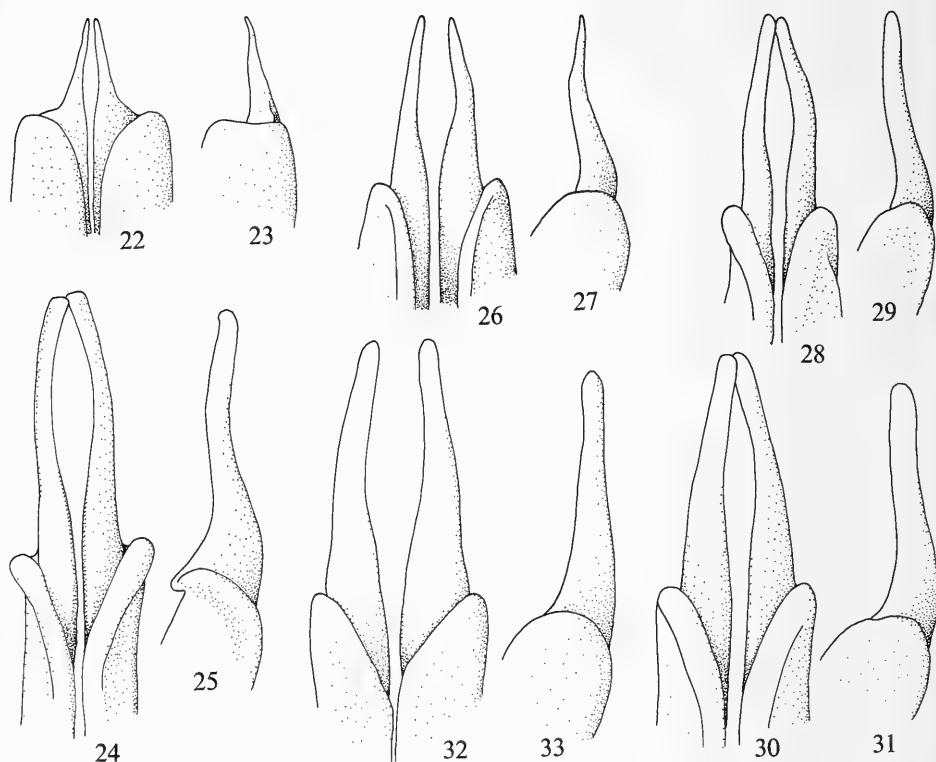
Material studied: ♂ holotype, labelled: N. Guinea, Type, *Cranæ unistrigata* De Haan ♂ Det. C. Willemse (RNH). The specimen lacks the left antenna and right fore leg.

### Redescription of the holotype.

Male, pl. 4 fig. 27. Differs from the type-species in head, pronotum, elytron, abdominal terminalia and coloration.

Head slightly more globose. Face wider. Lateral facial keels and margins of frontal ridge more raised. Interocular distance wider. Fastigium verticis more widely triangular, more declivous, and apex wider and not fissured.

Pronotum (pl. 2 fig. 11) slightly wider, dorsum more depressed and sulci less



Figs. 22—33. *Cranæ* species, ♂, tips of apical penis valves and sheath of penis, ventro-posterior (even numbers) and left lateral (odd numbers) view, similar scales; 22—23, *genjam* sp.n. (holotype); 24—25, *unistrigata* De Haan (holotype); 26—27, *unistrigata* (De Haan), Form 2 (Sorong); 28—29, *unistrigata* (De Haan), Form 4 (Jobi I.); 30—31, *unistrigata* (De Haan), Form 6 (Adelbert Mts.); 32—33, *rufipes* Ramme (?) (Toricelli Mts.).

wide. Elytron narrower and longer, reaching just beyond middle of hind femur. Furculae larger. Apex of phallus (figs. 24—25) longer and much more elongate; apical penis valves narrow, very slightly tapering apically, tips obtuse.

Coloration olivaceous green, yellow and black. Antennae dark brown. Head black except for olivaceous face and mouthparts, yellow fastigium verticis, a yellow sharply delimited, ovoid spot on the occiput near the dorso-posterior margin of each eye and a yellow narrow fascia from the antennal base along anterior margin of eye and lower margin of cheek.

Pronotum yellow with three black fasciae: a median one over the dorsum, twice as wide as each yellow lateral part of the dorsum and, on either side, over the upper two-thirds of lateral lobe. Meso- and metathorax yellowish, except for first episternum, upper part of pleurae and lateral parts of meso- and metasterna, which are black. Elytron brownish-black with a narrow yellow streak along folding of elytron. Hind wing slightly infumate. Abdomen brown, cerci and supra-anal plate darker brown.

Fore and middle legs olivaceous green. Hind femur in basal half olivaceous green, with fishbone pattern darker green, in distal half red with a yellow, narrow, antegenicular ring; lower inner marginal area completely red; inner medial area almost completely red. Hind knee, tibia and tarsus dark blue.

Measurements (length in mm): body, 19.0; pronotum, 3.8; elytron, 9.0; hind femur, 11.5.

Distribution: New Guinea (SW coast).

Discussion. Contrary to Ramme's (1941) statement, the holotype is in the collection of the Leiden Museum (C. Willemse, 1928, 1956). The agreement of the specimen with figure 7 in the original paper is conspicuous. The locality label reads "N. Guinea". In the original paper (p. 143) the locality is defined "Nieuw Guinea's zuid-westkust". The juvenile male of figure 8 in De Haan's paper could not be traced.

Comparison of the material at hand with the holotype of *unistrigata* reveals that a complex of closely related forms has been referred to that species previously. The differences in morphology and coloration are not conspicuous, but rather stable. It must be pointed out that when the material from different localities agrees in certain features, these localities always form a united section of the range of the whole complex. Due to the scanty morphological differences, especially in the shape of the apex of phallus, it is impossible to ascertain whether reproductive isolation has been achieved by the various populations. Only in one case, the quite distinct apex of phallus justifies the creation of a distinct taxon (*genjam*). The situation in the *unistrigata* complex can be compared with that in *Pseudocranae bimaculata* C. Willemse (F. Willemse, 1972: 53). I here arrange the material into six distinct Forms, of which Form 1 agrees with the holotype and Ramme's "*unistrigata* Färbungsrasse Mt. Arfak", Form 2 with Ramme's *caprai*, and Form 6 with Ramme's "*unistrigata* Färbungsrasse Sepik-Gebiet". The differences lie in the projecting ends of the apical penis valves and in the coloration. As to the latter, the yellow occipital spots, the width of the pronotal fasciae and the coloration of the legs, especially of the hind femur, appear to be of taxonomic value.

*Form 1*

*Cranae unistrigata*; Ramme, 1941: 90 (Färbungsrasse Mt. Arfak); C. Willemse, 1956: 107 (partim).

Material studied: Vogelkop, Fak Fak, S. Coast of Bomberai, 10—100 m, 12. vi. 1959, T. C. Maa (1 ♂) (MC); Fak Fak, C. J. L. Palmers (1 ♀, discoloured) (NMM); S. W. New Guinea, S. coast, Kambrau near Argoniibaai, 4. viii. 1941 (1 ♀) & near mouth of R. Aindoea, 12.viii. 1941 (1 ♀), E. Lundquist (NMM); Siwi (Forêt), 6.iii.1929, Prince Léopold (1 ♂) (NMM); Siwi, Arfak, 21.iv.—25.v.1928, Mayr (1 ♂, 1 ♀ ZMHU, 1 ♀ NMM).

The males of this material (all from Northwest New Guinea) agree fairly well with the holotype of *unistrigata*, especially in the apex of phallus.

The female, not yet described for *unistrigata* (s.l.), is larger than the male. Face, pl. 1 fig. 2. The tegmina are more separated dorsally and shorter than in the male. The elytron (pl. 3 fig. 18) is two-and-one-half times as long as wide, anterior margin moderately tapering apically. Abdominal terminalia as in the type-species. Dorsal aspect of subgenital plate and the spermatheca as in figs. 3—4. Coloration as in the male. Inner medial area of hind femur may be completely red, base of lower inner marginal area dark olivaceous. The measurements agree with those given by C. Willemse (1956). The Fak Fak material has not been recorded previously.

*Form 2*

*Cranae unistrigata*; I. Bolívar, 1898: 88 (only Sorong); C. Willemse, 1939: 75 (do); Kevan, 1966: 411 (do).  
*Cranae caprai* Ramme, 1941: 91, fig. 38; C. Willemse, 1956: 99, 107.

Material studied: Sorong, T. Barbour (1 ♂, 2 ♀) (ANSP); Nieuw Guinea Expeditie 1903, Manikion, 14.—28.II (1 ♂) (NMM) (all discoloured).

Ramme described *caprai* after a single discoloured female from Sorong. The present material from Sorong agrees with Ramme's description. However, most, if not all, distinct characters just may be due to shrivelling. The apex of phallus of the Sorong male (figs. 26—27) differs from that of the holotype of *unistrigata*, in shorter and more tapering apical penis valves with tips less obtuse. Whether this distinction is reliable is difficult to evaluate as the specimen, like the female, is shrivelled by spirit.

The present Sorong material has been referred to *unistrigata* by Kevan (1966), the Manikion male to *caprai* by C. Willemse (1956). The locality of the latter could not be traced. The apex of phallus of this male agrees with that of *unistrigata*'s holotype rather than with that of the Sorong male.

*Form 3*

*Cranae unistrigata*: I. Bolívar, 1898: 88 (only Waigiou); C. Willemse, 1939: 75 (do); 1956: 106 (do).

Material studied: Waigeou, Staudinger (1 ♀) (NMM).

Material from Waigou Island has been referred to *unistrigata* by I. Bolívar. A female of this material is at hand, bearing Bolívar's identification label. The

specimen differs from the female of Form 1 als follows: elytra shorter, reaching distal end of basal third of hind femur; subgenital plate flattened, not sulcate apically; occipital spots not ovoid, but elongate; fore and middle femora reddish; basal half of lower inner marginal area and fishbone pattern of outer medial area of hind femur black.

#### Form 4

*Cranæ unistrigata*: Kevan, 1966: 411 (Jobi I. only).

Material studied: Jobi Isl., Poue, T. Barbour (2♂, discoloured) (ANSP, MC).

Different from the holotype of *unistrigata* in the apical penis valves (figs. 28—29) which are much shorter. Like in Form 2, the difference is difficult to evaluate.

#### Form 5

Material studied: Biak I., 5 m, 26.ix.1958, *Pandanus*, J. L. Gressitt (1 juv.♂, 1 ♀) (BPBM).

The phallic complex of the juvenile male is not yet sclerotized. The coloration of the specimen is similar to that of the adult female. The latter differs from the female of Form 1 in the coloration as follows: general colour of face and legs not olivaceous green but yellowish-green; black fasciae of head and pronotum narrower; distal part of hind femur not sanguineous red but suffused orange. This form comes near the following one.

#### Form 6

*Cranæ unistrigata*: Ramme, 1941: 90 (Färbungsrasse Sepik-Gebiet); C. Willemse, 1956: 107 (partim).

Material studied: Neth. Ind.—Amer. New Guinea Exp. 1938—39, Hollandia, vii.1938, J. L. Toxopeus (2♀) & Bernhard Camp, 50 m, xii.1938, J. Olthof (1♀) (NMM); Neth. New Guinea, Waris, S. of Hollandia, 450—500m, 1—7.viii.1959, T. C. Maa (3♂) (BPBM); Kais. Wilhelmsland, Paup, 1910, Dr. Schlaginhaufen (1♀) (ZMHU); D.N. Guinea, Lager a. Töpferfluss, Kais. Augustafl. Exp., 29.iv.1912, Bürgers (1♀) & Standlager a. Aprilfl., 8—9.i.1912, Bürgers (1♂) (ZMHU); NE. New Guinea, Adelbert Mts., Wanuma, 800—1000 m, 27.x.1958, J. L. Gressitt (1♂, 1♀) (BPBM).

This group of specimens from several localities in the northern part of central New Guinea is uniform. It differs from Form 1 in the apex of phallus and in coloration. The apical penis valves are slightly shorter, wider basally and more tapering apically (figs. 30—31). The yellow occipital spots are conspicuously elongate, the black fasciae of head and pronotum narrower, fore and middle legs yellowish or olivaceous, hind femur yellowish or orange-yellowish and suffused with orange or orange-red distally; femur more marked in the male than in the female.

The material from Waris and Adelbert Mts. has not been recorded previously.

***Cranae genjam* sp.n.**  
(figs. 22—23, pl. 4 fig. 28)

Material studied: ♂ holotype, labelled: Neth., New Guinea, Genjam, 40 km W. of Hollandia, 100—200 m, 1—10.iii.1960, T. C. Maa (BPBM).

**Description.**

Male, pl. 4 fig. 28. Differs from *unistrigata* as follows: face less wrinkled, furculae larger, apical penis valves much shorter, wider basally and more strongly tapering apically (figs. 22—23). Coloration much as in the holotype of *unistrigata* except for the pronotum and hind femur. The black median fascia over pronotal dorsum narrower, as wide as each of the yellow lateral parts of the dorsum. The sanguineous distal part of hind femur much shorter, not extending over the inner lower marginal and inner medial areas and better defined.

Female. Unknown.

Measurements (length in mm): body, 20.5; pronotum, 4.3; elytron, 9.1; hind femur, 11.6.

Distribution: New Guinea (Genjam, near Hollandia).

Discussion. The species is well-defined by its resemblance to nominate *unistrigata* in combination with its different apical penis valves. As to this character, *genjam* is related with *tibialis* and *patagiata*.

***Cranae trivittata* C. Willemse, 1922**  
(pl. 2 fig. 12)

*Cranae trivittata* C. Willemse, 1922: 714, fig. 5; 1939: 75; F. Willemse, 1966a: 38; 1966b: 65 (Bivak Eiland only).

*Cranae trivittata trivittata*: Ramme, 1941: 92; C. Willemse, 1956: 99, 105 (partim).

Material studied: ♀ holotype, labelled: Z. Nieuw Guinea Lorentz 1909 - 10 Kloofbivak (ITZ).

Additional material: Z. Nieuw Guinea, Bivak Eiland, 1909—10, Lorentz (1 ♀) (NMM).

**Redescription.**

Male. Unknown.

Female. Differs from the type-species as follows. Head comparatively larger and rather more globose. Interocular distance wider. Fastigium verticis widely triangular, more declivous, apex wider. Pronotum (pl. 2 fig. 12) shorter, sulci weaker; dorsum more depressed, prozona, in profile, slightly upcurved; lateral lobe shorter than high, posterior margin slightly concave. Elytron slightly longer, reaching about middle of hind femur, apex narrower. Ovipositor valves more slender.

Coloration as described in the original paper. Marked characters are: head pale olivaceous green, with a black postocular fascia, yellow fascia along anterior margin of eye and lower margin of cheek and a pair of yellow, elongate-ovoid



spots from between the eyes, almost reaching pronotum; pronotum yellow with black fascia over upper part of lateral lobe and a median one over the dorsum, the width of the latter almost equal to the width of either yellow, lateral part; elytron black with yellow streak over the folding of elytron, at its base as wide as the yellow lateral part of pronotal dorsum; fore and middle legs and hind femur pale olivaceous green, the latter with fishbone pattern black, an ivory-white antegenicular ring, which is bordered by a narrow, complete, blackish ring proximally (see original paper, fig. 5).

Measurements (length in mm): body, 26.0—27.0; pronotum, 4.5—5.0; elytron, 8.8—9.0; hind femur 14.7—15.1.

Distribution: SW New Guinea (Kloofbivak and Bivakeiland).

Discussion. The large head, short pronotum and coloration are distinct characters. However, the male being unknown, the species cannot be properly defined. The external morphology is much as in the *unistrigata* group. The coloration resembles that of *rufipes* and *manokwari*.

### ***Cranae rufipes* Ramme, 1941**

(figs. 32—33, pl. 2 fig. 13)

*Cranae trivittata rufipes* Ramme, 1941: 92; C. Willemse, 1956: 99, 106; 1962: 64.

*Cranae trivittata trivittata*: C. Willemse, 1956: 105 (partim) (?).

Material studied: ♀ holotype, labelled: Deutsch Neu Guinea (ZMHU).

Additional material: NE New Guinea, Huon Peninsula, Finschhafen, 10 m, 16.iv.1963, J. Sedlacek (1 ♀) (BPBM); Nouv. Guinée, Baie Triton, 1841, Jacquinot (1 ♀) (MNHN).

#### Redescription.

Male. Unknown (?), see below.

Female. Differs from the type-species in the slightly more globose head, wider interocular distance, more widely triangular fastigium verticis with wider apex and the slightly shorter elytra with narrower apex. Differs from *trivittata* in the less globose head and longer pronotum (pl. 2 fig. 13), with the dorsum less depressed and the prozona not upcurved.

Coloration differing from that in *trivittata* as follows: black median fascia over pronotal dorsum slightly wider, nearly one-and-a-half times as wide as width of either, yellow, lateral part of the dorsum; fore and middle femora reddish; hind femur with antegenicular ring slightly wider and olivaceous green, bordered proximally with a black ring, which is incomplete on the outer side.

Measurements (length in mm): body, 30.0–30.2; pronotum, 5.5–5.6; elytron, 7.5–7.9; hind femur, 14.0–14.9.

Distribution: NE New Guinea (Finschhafen and Triton Bay).

Discussion. Like *trivittata*, the taxon is not well-defined. The morphological distinction between *rufipes* and *trivittata* is clear enough to raise *rufipes* to specific rank. The Finschhafen female agrees completely with the holotype, while the female from Triton Bay differs slightly in general colour, which is more orange-

yellowish, and in the width of the antegenicular ring of hind femur, which is as narrow as in *trivittata*.

The following material is at hand: Kais. Wilhelmsland, Toricelli Gebirge, 1910, Dr. Schlaginhaufen (1 ♂, 1 ♀) (NMM); Neth. New Guinea, Waris, S. of Hollandia, 450—500 m, 16—23.viii. 1959, T. C. Maa (2 ♀) (BPBM). The morphology of this female material is very similar to that of the holotype of *rufipes*. However, the coloration is slightly different: fore and middle femora olivaceous yellow, black ring of hind femur complete, well-marked and as narrow as in *trivittata*, fishbone pattern of hind femur unicolorous with hind femur and yellow streak over elytron narrower.

By evidence of similarity, the pair from Toricelli Mts. is considered conspecific. The phallic complex of the male is much as in *unistrigata*, but the apical penis valves are much wider (figs. 32—33). The two specimens were referred to nominate *trivittata* by C. Willemse (1956). However, I am not certain whether this material represents *rufipes* or a distinct taxon.

#### ***Cranae manokwari* sp.n.**

(figs. 34—35, pl. 3 fig. 19, pl. 4 fig. 29)

Material studied: ♂ holo-, ♀ allotype, labelled: New Guinea, Manokwari, Tafelberg 150 m 22.11.63 R. Straatman (BPBM).

#### **Description.**

Male, pl. 4 fig. 29. Differs from the type-species as follows: head more globose, interocular distance and fastigium verticis wider, elytron narrower with anterior margin more evenly rounded; apical penis valves (figs. 34—35) rather tapering apically, tips tooth-shaped and slightly outcurved.

Coloration as in *rufipes*, but vertex between the eyes and occiput completely black with two small, ovoid, yellow spots as in nominate *unistrigata*; median black fascia of pronotal dorsum slightly wider and fore and middle femora olivaceous yellow.

Female. Elytron, pl. 3 fig. 19. Abdominal terminalia as in type-species. Coloration as in male, except upper side of head which is more yellowish-brown with occipital spots faintly indicated.

Measurements (length in mm): body, ♂ 22.4, ♀ 30.3; pronotum, ♂ 4.4, ♀ 5.1; elytron, ♂ 7.8, ♀ 8.2; hind femur, ♂ 11.9, ♀ 14.0.

Distribution: NW New Guinea (Tafelberg near Manokwari).

Discussion. The species is well-defined by the apex of phallus and the coloration. It appears to be closely related to *rufipes*.

#### ***Cranae longipennis* sp.n.**

(figs. 14—15, 36—37, pl. 1 fig. 4, pl. 3 fig. 20, pl. 5 fig. 31)

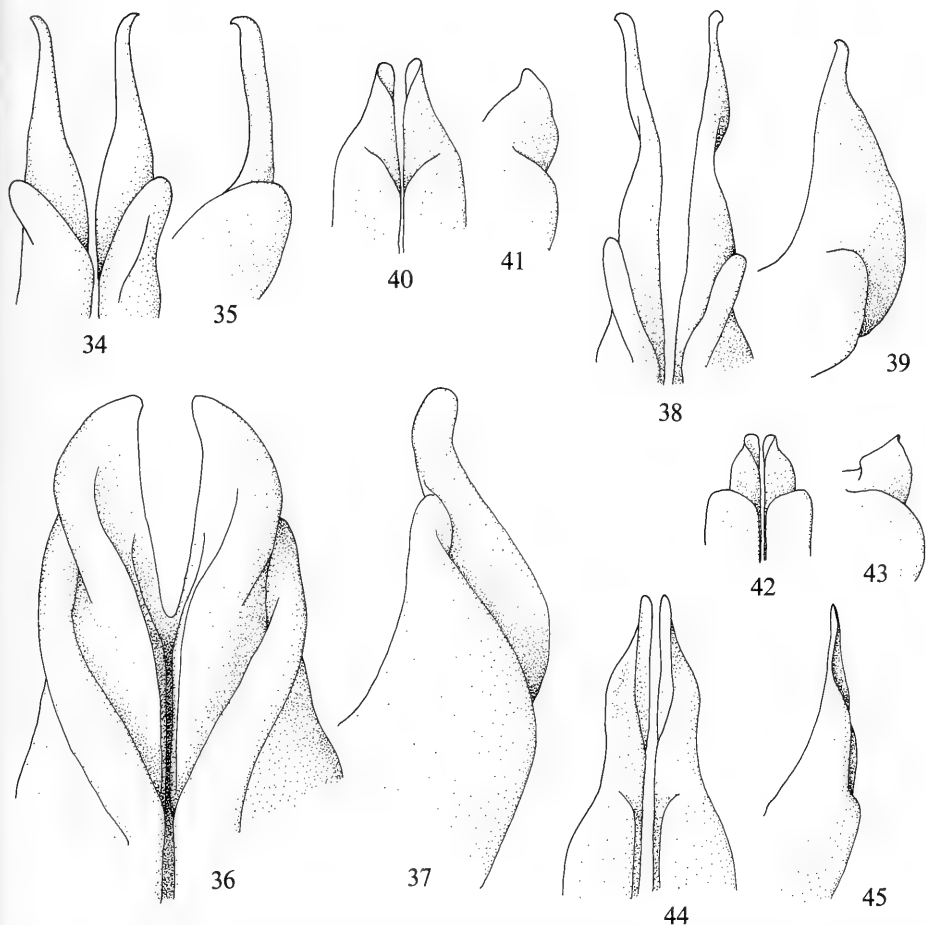
Material studied: ♂ holotype, ♀ allotype, labelled: Papua, Fly R. Olsabip 400—800 m, viii. 69, J. & M. Sedlacek (BPBM); paratypes: Neth. New Guinea Exp. Star Range, Katem 200 m, 15.vi.1959 (2 ♂) (RNH).

## Description.

Male, pl. 5 fig. 31. Differs from the type-species in body, head, tegmina, abdominal terminalia and coloration. Body of larger size and more robust. Face wider and more wrinkled. Fastigium verticis and interocular distance wider. Tegmina longer, reaching end of middle third of hind femur. Elytron about three times as long as wide and less tapering. Cerci more pointed and robust.

Phallic complex very large. Ancorae of epiphallus (figs. 14—15) partly joined with the lateral plates. Apex of phallus (figs. 36—37) very robust, sheath of penis conspicuously developed, tips of apical penis valves shell-shaped.

Coloration black, bluish-green, blue and yellow. Antennae blackish. Head greenish-black with following parts cadmium-yellow: sulcus of fastigium verticis



Figs. 34—45. *Cranae* species, ♂, tips of apical penis valves and sheath of penis, ventro-posterior (even numbers) and left lateral (odd numbers) view, similar scales; 34—35, *manokwari* sp.n. (holotype); 36—37, *longipennis* sp.n. (holotype); 38—39, *rubra* sp.n. (holotype); 40—41, *kuekentali* Brunner (paratype); 42—43, *luctuosa* C. Bolívar (Telaga, Obi I.); 44—45, *pictipennis* C. Willemse (allotype).

and frontal ridge, scape, deep and symmetrical impressions of face, face along lateral keels and cheek along lower margin, the mouthparts partly, and a narrow stripe along dorso-posterior margin of eye. Pronotum yellow with three, longitudinal, wide, black fasciae: on each side, over the upper two-thirds of lateral lobe and a median one over the dorsum, being about twice as wide as the yellow lateral parts of the dorsum. Rest of thorax yellowish with episternum, upper part of pleurae and margins and sutures of meso- and metasterna black. Elytron black with wide, median, cadmium-yellow streak. Hind wing infumate. Abdomen yellowish-brown, tergites laterally suffused green. Cerci and a median stripe on supra-anal plate yellow. Fore and middle legs dark green with yellow streaks. Hind femur yellowish or olivaceous green, carinae and fishbone pattern dark olivaceous or bluish-green, inner lower marginal area completely dark blue. Hind knee dark blue with yellowish-white antegenicular ring, which is shorter than length of hind knee and incomplete ventrally. Hind tibia and tarsus bluish-black, tibia with a narrow, yellowish-white, postgenicular ring, hind tarsus yellowish laterally.

Female. Larger than the male. Face, pl. 1 fig. 4. Elytron, pl. 3 fig. 20. Abdominal terminalia as in the type-species, but more robust. Coloration as in the male.

Measurements (length in mm): body, ♂ 24.0—26.0, ♀ 33.2; pronotum, ♂ 4.6—5.0, ♀ 6.3; elytron, ♂ 11.3—11.6, ♀ 12.3; hind femur, ♂ 12.5—12.7, ♀ 16.0.

Distribution: S. New Guinea (Katem, Star Range and Olsabip, Fly River).

Discussion. The species is very distinct. Shape and measurements of tegmina and phallic complex are conspicuous. The species seems related to the *unistrigata* complex rather than to other species.

### ***Cranae rubra* sp.n.**

(figs. 38—39, pl. 5 fig. 32)

*Cranae patagiata*; Krauss, 1903: 747, 759 (British New Guinea) (?)

*Cranae* sp. aff. *patagiata*; Kevan, 1966: 410 (not Normanby I.).

Material studied: ♂ holotype, ♀ allotype, ♀ paratype, labelled: New Guinea: Papua Woodlark I (Murua) Kulumadaw Hill, Mar. 19—22. 1957, W. W. Brandt, *Cranae patagiata* St.? det. D. K. mcE. Kevan, 1965 (BPBM).

### **Description.**

Male. (pl. 5 fig. 32). Differs from the type-species as follows: pronotum narrower and shorter with dorsum more depressed and sulci slightly stronger; legs slightly more slender; apical penis valves (figs. 38—39) long, flattened laterally, tips slightly pointed and recurved.

Coloration black, carmine and yellow. Head and thorax as in *unistrigata*, but occipital spots smaller. Elytron carmine, anterior margin widely, posterior margin narrowly bordered with black. Abdomen and legs as in type-species, except for the hind femur. Hind femur in basal half carmine, in distal half blackish-red with a yellow antegenicular ring, which is almost twice as long as the length of hind knee.

Female. Larger than the male. Abdominal terminalia as in the type-species. Coloration as in the male, but face more unicolorous yellow.

Measurements (length in mm): body, ♂ 18.9, ♀ 23.6—24.5; pronotum, ♂ 3.6, ♀ 4.5—4.8; elytron, ♂ 8.2, ♀ 8.2—8.4; hind femur, ♂ 11.7, ♀ 13.0—13.5.

Distribution: New Guinea (Papua: Woodlark I.).

Discussion. The species is well-defined by the apex of phallus and the coloration. Although the coloration is much as in *patagiata*, the species agrees more closely with the *unistrigata* complex. The material studied by Krauss was not at hand.

***Cranea kuekenthali* Brunner, 1898**

(figs. 11—13, 40—41, pl. 3 fig. 21)

Ramme (1941) distinguished two subspecies, viz., *kuekenthali* and *annulata*. The nominate form occurs in the northeastern part of Halmahera, *annulata* in the western part of that island. Distinction was based on different coloration of the hind femur. Ramme, in the same paper, synonymized the male of *Cranea marginata* Brunner with nominate *kuekenthali*. Neither the type of *marginata*, nor that of *annulata* or nominate *kuekenthali* could be studied (deposited in the Senckenberg Museum Frankfurt). The only material available for the present study are a paratypic male of nominate *kuekenthali* and some discoloured material, labelled: Halmahera, T. Barbour (1♂, 2♀ ANSP, 1♂ MC). As to the discoloured material, agreement with *kuekenthali* is apparent, but subspecific distinction is impossible. For the time being, no comments are given on Ramme's opinion.

***Cranea kuekenthali kuekenthali* Brunner, 1898**

*Cranea kuekenthali* Brunner, 1898: 198, 238, pl. 18 fig. 136 (partim); Kirby, 1910: 387; C. Bolívar, 1923: 146; C. Willemse, 1939: 74; Ramme, 1941: 88, 89; Kevan, 1966: 411.

*Cranea kuekenthali kuekenthali*; Ramme, 1941: 89; C. Willemse, 1956: 98, 102.

*Cranea marginata* Brunner, 1898: 198, 236, 237 (partim); Kirby, 1910: 387; C. Willemse, 1939: 74; Ramme, 1941: 87, 89 (♂ synonymy established); C. Willemse, 1956: 102 (in synonymy only).

Material studied: 1♂ paratype, labelled: Halmaheira 1894 W. Kükenthal leg., Paratypus (ZMHU).

**Redescription.**

Male. Differs from the type-species as follows. Integument of face and pronotum smoother, scarcely pitted. Head larger; face less wrinkled, wider and slightly depressed along lateral keels. Pronotum shorter, more cylindrical (dorsum less depressed), in the middle slightly compressed laterally; sulci stronger; lateral lobe not as long as high, posterior angle slightly pointed. Elytron shorter, reaching about end of basal fourth of hind femur, about twice as long as wide, anterior margin evenly and widely rounded, archedyection conspicuous. Furculae slightly larger and closer together. Cercus more slender and extending slightly beyond tip of subgenital plate. Ancorae of epiphallus not joined with lateral plates (fig. 11). Cingular rami much wider (figs. 12—13). Apex of phallus shorter, roughly conical, tip of penis valves excavated medially (figs. 40—41).

Coloration as given in the original paper. Marked characters are summarized as follows: head yellow with wide, black, postocular fascia and narrower, black stripe

from between eyes over occiput, widening posteriorly; pronotum black, margins bordered with yellow, along anterior margin of dorsum widened into a pair of yellow spots; elytron yellowish, apex and apical part of anterior margin bordered with black; femora orange-red, the hind one apically more yellowish and with a narrow, black ring placed just distally of middle of hind femur; hind knee blackish; hind tibia bluish suffused with yellowish.

Female. Larger than male. Subgenital plate flattened, between the keels not sulcate. Elytron as in pl. 3 fig. 21, in other specimens the black pigmentation may extend more anteriorly. Coloration as in the male.

Measurements (length in mm): body, ♂ 21.0—22.0, ♀ 29.0—29.5; pronotum, ♂ 4.1—4.4, ♀ 5.5—5.7; elytron, ♂ 5.6—5.8, ♀ 5.2—5.3; hind femur, ♂ 12.4—12.6, ♀ 15.2—15.6.

Distribution: Moluccas (Halmahera).

Discussion. The species is well-defined by the external morphology, the phallic complex and the coloration. The description of the female has been made after the discoloured material recorded above (ANSP, MC). Whether the not sulcate female subgenital plate is a reliable character is not certain, as the material is shrivelled. A figure of the phallic complex is also given by Kevan (1966, Pacific Insects 8: 697, fig. 2) under the name *Cranae kuekenthali* (nec I. Bolívar). The species, together with *luctuosa*, forms a group (see below under *luctuosa*).

### ***Cranae kuekenthali annulata* Ramme, 1941**

*Cranae kuekenthali* Brunner, 1898: 198, 236, 238, pl. 18 fig. 36 (partim).

*Cranae kuekenthali annulata* Ramme, 1941: 89; C. Willemse, 1956: 99, 102; Kevan, 1966: 411.

No comments are given because of lack of material.

### ***Cranae luctuosa* C. Bolívar, 1923**

(figs. 42—43, pl. 1 fig. 5, pl. 2 fig. 14, pl. 3 fig. 22, pl. 4 fig. 30)

*Cranae luctuosa* C. Bolívar, 1923: 145; C. Willemse, 1939: 74; 1956: 99, 103; F. Willemse, 1966b: 64.

Material studied: 1 ♂ paratype, labelled: Moluques Obi Major J. Waterstradt 1902 (NMM).

Additional material: Obi I., Telaga, 3 & 4 & 25 & 26.viii. 1953 (4 ♂, 1 ♀ NMM; 1 ♂, 1 ♀ RNH); Obi I., Laiwui, 27.ix.1953 (1 ♀) (NMM).

#### **Redescription.**

Male, pl. 4 fig. 30. Differs from *kuekenthali* as follows. Head larger, more globose. Pronotum, pl. 2 fig. 14; posterior margin of lateral lobe slightly concave. Elytron longer, about three times as long as wide, anterior margin less widely rounded. Supra-anal plate slightly wider and shorter, transverse ridges more distinct. Cerci longer, extending well beyond tip of subgenital plate. Apex of phallus slightly smaller and less conical (figs. 42—43).

Coloration as described by C. Willemse (1956). Marked characters are as

follows. Head from pale yellow to olivaceous yellow, with the following parts bluish-black: a transverse stripe over the face below the antennae, a wider one along clypeal margin and lower margin of cheek, more or less the whole cheek, the area behind the eye, a median stripe over the occiput and the posterior part of the latter. Thorax bluish-black, margins of pronotum yellow or, usually, as spotted yellow: a median one on the anterior margin of the dorsum and the others on the anterior and posterior angles of the lateral lobe. Elytron yellowish-white, apex and apical part of anterior margin bordered with black. Fore and middle legs olivaceous green, more or less suffused with bluish. Hind femur in proximal two-thirds bluish-black, in distal third yellow. Hind knee and tibia bluish-black.

Female. Larger than the male. Face, pl. 1 fig. 5. Elytron, pl. 3 fig. 22. Abdominal terminalia as in *kuekenthali*. Coloration as in the male, but head, pronotum and hind femur less black and occasionally almost completely yellowish.

Measurements as given by C. Willemse (1956).

Distribution: Moluccas (Obi I.).

Discussion. The species is well-defined by morphology and coloration. Its resemblance to *kuekenthali* is striking. Both species are characterized, among *Cranae*, by smoother integument, shorter and more cylindrical pronotum with deeper sulci and another type of phallic complex. In these characters, the two agree with *Opiptacris* Walker rather than with *Cranae*. However, the developed tegmina and the open tympanum do not agree with *Opiptacris*.

### ***Cranae glabra* sp.n.**

(pl. 1 fig. 6, pl. 2 fig. 15, pl. 3 fig. 23, pl. 5 fig. 33)

Material studied: ♀ holotype, 1 ♀ paratype, labelled: Neth. New Guinea: Biak I.: Kampong Landbouw, 50—100 m, May 27, 1959, J. L. Gressitt; 1 ♀ paratype: Biak I. (Neth. N. Guinea) SE coast 5 m, xi—26—1958, *Freycinetia*, J. L. Gressitt; 1 juvenile ♂ Neth. New Guinea; Biak I., Mokmer 5—10 m, v—26—1959, J. L. Gressitt (all BPBM).

#### **Description.**

Male. Cerci of the juvenile male long, extending well beyond tip of subgenital plate. Phallic complex not sclerotized. Coloration pale yellowish.

Female, pl. 5 fig. 33. Differs from the type-species as follows. Body more slender, integument much smoother. Face (pl. 1 fig. 6) not wrinkled and comparatively narrow. Pronotum (pl. 2 fig. 15) shorter, more cylindrical, in the middle slightly laterally compressed, sulci stronger, posterior angle of lateral lobe slightly pointed and posterior margin slightly concave.

Elytron (pl. 3 fig. 23) smaller, much narrower, three times as long as wide, reaching middle of second abdominal tergite, both elytra widely separated dorsally; anterior margin slightly rounded, posterior margin straight, distally tapering towards narrow, undivided, parabolic apex; veins rather reduced, not by far reaching anterior margin. Hind wing almost as long as elytron. Tympanum as usual. Legs slender, hind femur attenuate, fishbone pattern and keels moderately developed. Subgenital plate flattened, not sulcated between low keels.

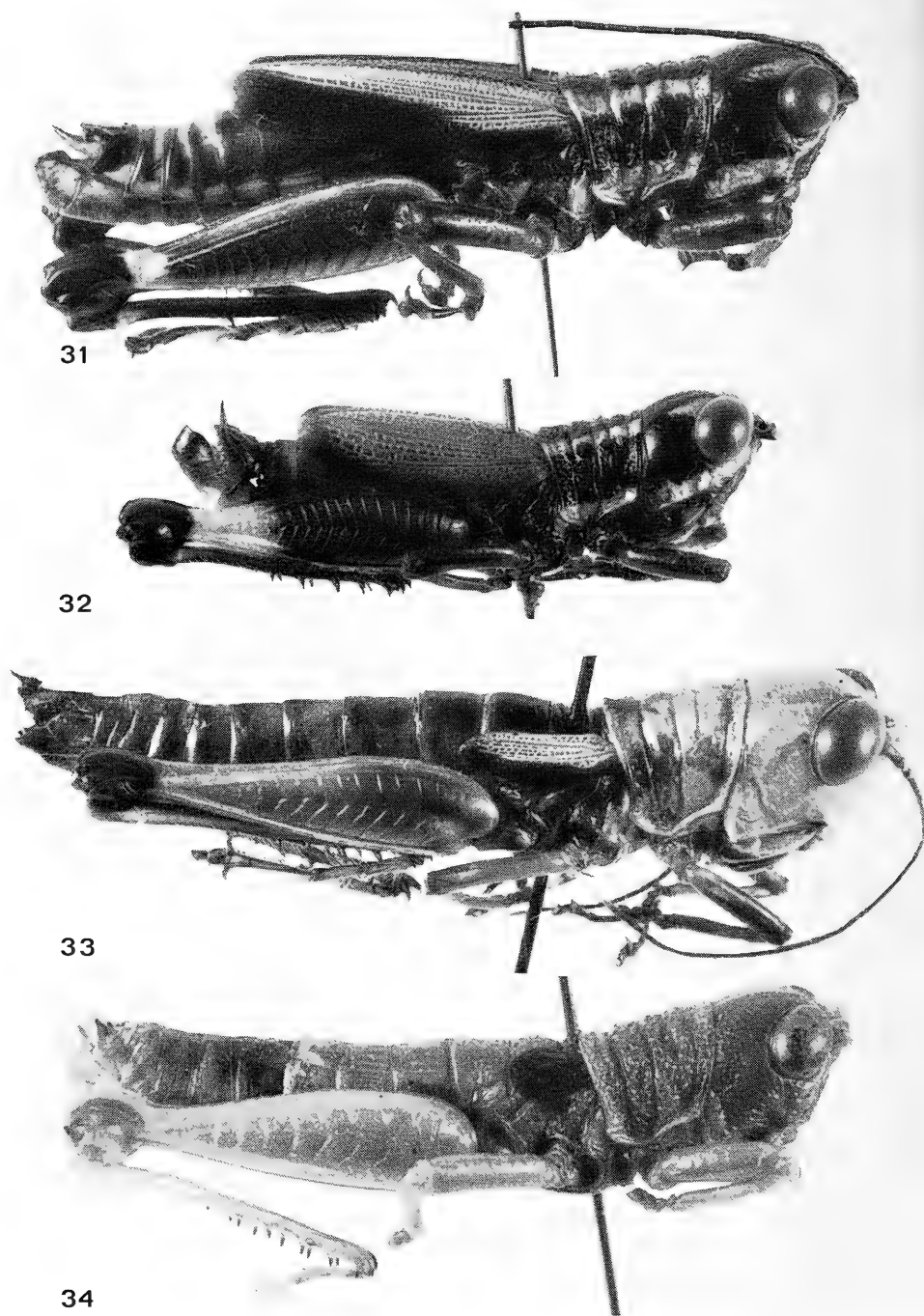


Plate 5. Figs. 31—34. *Craea* species, lateral view: 31, *longipennis* sp.n., ♂ (holotype); 32, *rubra* sp.n., ♂ (holotype); 33, *glabra* sp.n., ♀ (holotype); 34, *pictipennis* C. Willemse, ♂ (allotype).



Coloration yellowish and orange-brown. Antennae dark brown, apically paler. Head yellowish, mouthparts mottled with bluish-green. Pronotum orange-brown with three narrow, bluish-green fasciae: on each side over upper part of lateral lobe and a median one over dorsum; these fasciae are widest along anterior and posterior margins of pronotum, and almost obsolete near the middle of pronotum. Pleurae with lower part orange-brown, upper part bluish-black. Pro-, meso- and metasterna brownish. Elytron yellow, anterior margin broadly bordered with black. Abdomen brown, proximal tergites blackish brown. Coxae orange-brown. Fore and middle legs orange-brown, tibiae suffused with bluish-green. Hind femur orange-brown, lower inner marginal area bluish, outer side basally slightly suffused with dark brown. Hind knee, tibia and tarsus dark blue or bluish-green.

Measurements (♀ length in mm): body, ♂ 27.8–28.3; pronotum, 4.7–4.8; elytron, 5.1–5.8; hind femur, 13.8–14.6.

Distribution: New Guinea (Biak I.).

Discussion. Although the adult male is not known, the species is well-defined. Both morphology and coloration are quite distinct. Integument, head, pronotum and female abdominal terminalia agree with *kuekenthali* and *luctuosa*. These features agree with *Opiptacris* Walker rather than with *Cranae*. Besides, the tegmina in *glabra* are much as in some species of *Cranaella* Ramme (compare F. Willemse, 1977: 110). Apparently, *Cranae glabra* is more or less intermediate between *Cranae*, *Cranaella* and *Opiptacris*.

### ***Cranae pictipennis* C. Willemse, 1932**

(figs. 44–45, pl. 1 fig. 7, pl. 2 fig. 16, pl. 3 fig. 24, pl. 5 fig. 34)

*Cranae pictipennis* C. Willemse, 1932: 279; 1939: 74; F. Willemse, 1966a: 38; 1966b: 64; 1976: 121 (original combination re-established).

*Opiptacris pictipennis*; Uvarov, 1937: 17, 18; C. Willemse, 1956: 95.

Material studied: type-series, labelled: Buru, Station Nal Besi (♀ paratype, RNH) & Station 16 (♀ holotype, RNH) & Station 7 (♂ allotype, NMM), 1921, leg. L. J. Toxopeus, *Cranae pictipennis* nov. sp. det. C. Willemse, *Opiptacris pictipennis* Will. det. C. Willemse, type-labels. The specimens are discoloured.

### **Redescription.**

Male, pl. 5 fig. 34. Differs from the type-species as follows. Body more robust. Integument of face and pronotum (pl. 2 fig. 16) strongly pitted. Pronotum with sulci less deep, posterior angle of lateral lobe obtusely pointed, posterior margin slightly concave laterally, slightly emarginate dorsally. Tympanum closed, as a narrow, hour-glass-shaped furrow. Elytron very short, reaching first abdominal tergite, roughly circular with apex broadly rounded to almost truncated, venation obsolete. Hind wing represented by a small membrane. Phallic complex as in type-species, except for its apex. Sheath of penis not strongly folded apically but more gradually merging into apical penis valves (figs. 44–45); the latter tapering apically and excavated medially.

Coloration. The material is strongly discoloured. Elytra, apex of mandible,

crescents of hind knee and furculae of the male, all black. A faintly retained pattern on the head and pronotum is much as in *kuekenthali*.

Female. Larger than the male. Face, pl. 1 fig. 7. Elytron, pl. 3 fig. 24. Abdominal terminalia about as in the type-species. Coloration as in the male.

Measurements (length in mm): body, ♂ 25.1, ♀ 28.1—32.0; pronotum, ♂ 4.7, ♀ 5.3—5.3; elytron, ♂ 2.6, ♀ 2.8—3.0; hind femur, ♂ 13.4, ♀ 14.8—15.1.

Distribution: Moluccas (Buru).

Discussion. The species is well-defined morphologically. In the tegmina and tympanum it agrees with *Opiptacris* Walker. However, the integument and especially the phallic complex disagree strongly with that genus. The integument is much as in *Cranaella* Ramme. As in the case of *glabra* and the *kuekenthali-luctuosa* group, *pictipennis* forms a link between *Cranae*, *Cranaella*, and *Opiptacris*.

### **Cranae emendata Brunner, 1898**

*Cranae emendata* Brunner, 1898: 196, 236, 237; Kirby, 1910: 387; C. Willemse, 1939: 74; Ramme, 1941: 92; C. Willemse 1956: 98, 99

The species is known after a single, discoloured female from Borneo. The type is in the Senckenberg Museum, Frankfurt, and not at hand. As no further material of the genus is known from Borneo, the record certainly needs confirmation.

The following five species are briefly described but pending the discovery of the male, no species name is proposed.

### **Cranae sp.**

Material studied: NE. New Guinea, Aseki, 19.xii.1965, H. Pyka (1 ♀) (author's collection).

Near *longipennis*. Body robust, face wide and strongly wrinkled. Pronotum rather depressed from above, tegmina wide and long, reaching beyond the middle of hind femur. General colour black; yellow stripes over head and pronotum as in *unistrigata*, but wider; elytron with a broad yellow streak; all femora red, the hind one with a yellow antegenicular ring and yellow streaks, one over the upper marginal areas and another along the lower outer carinula; hind knee black; all tibiae blackish, suffused with red.

### **Cranae sp.**

*Cranae* sp. aff. *patagiata*; Kevan, 1966: 410 (Normanby I. only).

Material studied: Papua, Normanby I., Wakaiuna, Sewa Bay 1—10.xi.1956, M. W. Brandt (2 juv. ♂, 1 ♀) (BPBM).

Near *trivittata*, *rufipes* and *manokwari*. Head about as large as in *trivittata*, pronotum about as in *rufipes*. Phallic complex of juvenile males not yet sclerotized.

Coloration as in *rufipes*, except for the legs. Fore and middle legs olivaceous. Hind femur scarlet red with a broad, yellow antegenicular ring, bordered proximally by a narrow black incomplete ring. Hind femur much as in *rubra*.

### *Cranae* sp.

Material studied: NE New Guinea, Bubia, Markham R., 50 m, 20.ix.1955, J. L. Gressitt (1 ♀) (BPBM).

Near *manokwari* but differing by more globose head and coloration of hind leg. Hind femur olivaceous green, fishbone pattern bluish-black, antegenicular ring orange-red, bordered proximally by a black dorsal spot. Hind knee and tibia dark blue.

### *Cranae* sp.

*Cranae unistrigata*; C. Willemse, 1956: 106 (Sabang only).

Material studied: Nieuw Guinea, Sabang vii.1907, Lorentz (1 ♀) (NMM).

Near *unistrigata*, but differing by more robust body, shorter pronotum and coloration. Black fasciae of head and pronotum conspicuously narrower, median one as wide as each of the yellow lateral parts of dorsum. Yellow streak over elytron much wider. Hind femur yellow, fishbone pattern dark olivaceous, yellow antegenicular ring narrower and bordered proximally by a narrower, well-marked red ring.

### *Cranae* sp.

*Cranae unistrigata*; Kevan, 1966: 411 (Roon I. only).

Material studied: D. N. Guinea, Roon Isl., Thomas Barbour (1 ♀) (ANSP). The specimen is discoloured.

Near *unistrigata*, but rather more robust and head remarkably large and globose. The discoloration being incomplete, the following pattern is still recognizable: between the eyes a pair of black spots, behind the eye a wide black fascia, pronotum unicolorous except for the central area of lateral lobe, which is darker. Elytron as in *unistrigata*.

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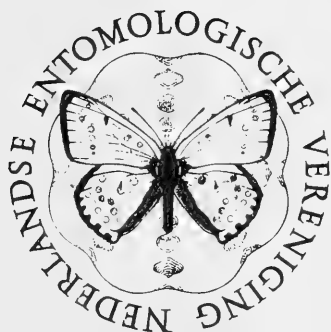
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## INHOUD

- J. C. ROSKAM. — Biosystematics of insects living in female birch catkins. I. Gall midges of the genus *Semudobia* Kieffer (Diptera, Cecidomyiidae), p. 153—197, text-figs. 1—122.





# BIOSYSTEMATICS OF INSECTS LIVING IN FEMALE BIRCH CATKINS. I. GALL MIDGES OF THE GENUS *SEMUDOBIA* KIEFFER (DIPTERA, CECIDOMYIIDAE)

by

J. C. ROSKAM

*Division of Systematics and Evolutionary Biology, University of Leiden, The Netherlands*

With 122 text-figures

## ABSTRACT

Five species of *Semudobia* Kieffer have been studied in their developmental stages. All stages are described and keys are provided. A neotype is designated for *Cecidomyia betulae* Winnertz, 1853, from *Betula pendula* (fruit galls), The Netherlands, and four new species are described, viz., *Semudobia brevipalpis* from *Betula papyrifera* (fruit galls), Canada, Quebec; *S. steenisi* from *B. occidentalis* (fruit galls), U.S.A., Wyoming; *S. tarda* from *B. pendula* (fruit galls), The Netherlands; and *S. skuhravae* from *B. pendula* (bract galls), The Netherlands.

## INTRODUCTION

In this paper, the first of a series on the entomofauna of female birch catkins, the galls, morphology and life cycle of five species of gall midges of the Holarctic genus *Semudobia* Kieffer are studied. In a second publication, now in preparation, morphology, life cycle and host relations of some of the hymenopterous parasites of these midges will be discussed. Finally, a "food web" will be constructed and attention will be paid to phylogenetic aspects of host-parasite relations of the species under study.

The first description of *Semudobia betulae* was published by Winnertz in 1853. He placed it in the genus *Cecidomyia* Meigen. Rübsaamen (1891) transferred the species to his genus *Hormomyia*. Kieffer (1895) originally placed it in the genus *Oligotrophus* Latreille, but in 1913 he made it the type-species of a new genus *Semudobia*. Although a rather recent review was given by Barnes (1951), it is necessary to discuss the literature in detail on certain topics. In fact these topics anticipate the splitting of the only described species in the genus.

Data on the number of antennal segments. — A mistake was made in the original description by Winnertz (1853). Although there may be some variation in the number of segments of the flagellum, the formulae  $2 + 10/11$  in the males (2 means scape plus pedicel, the other number is given for the segments of the flagellum) and  $2 + 10$  in the females, as indicated by Winnertz, are highly uncommon in *Semudobia*. Löw (1878) criticized these numbers, but unfortunately his counts (males  $2 + 12$ , females  $2 + 13$ ) do not fit either, because males in

*Semudobia* usually have one segment more than females. Barnes (1951) had also problems with the number of antennal segments, as for the females he recorded  $2 + 12$ , "but occasionally (—)  $2 + 15$ ", which must be an error for  $2 + 13$ . The data given by Rübsaamen (1891), Theobald (1892) and Kieffer (1913b) are correct:  $2 + 12/14$  (♂),  $2 + 11/13$  (♀).

Gall inducing and gall form. — Winnertz described *C. betulae* after specimens reared by Kaltenbach from female catkins of *Betula alba* L. from the preceding year. Neither Winnertz (1853) nor Kaltenbach (1874) did note that the midge was a gall inducer. In fact, the statements by Kaltenbach (1874) and Binnie (1877) are very confusing. They reported that the larvae live and pupate "in the interstices between the scales", although Binnie also observed the "inside of a seed" as a common position of the larva. Löw (1878), and later Wachtl (1881), were the first to study the behaviour of *Semudobia* carefully.

Löw criticized Kaltenbach (1874) heavily, considering "diesbezügliche Beobachtungen als äusserst oberflächlich", and observed the larvae of *Semudobia* enclosed in galls. Löw and Wachtl both described the galls; they reported at least two different gall forms but did not attribute these to different gall inducing species. Rübsaamen (1891) added a third gall form to those described by Löw and Wachtl, but did not suppose it to be due to a different gall inducing species either. A remarkable mistake was made by Connold (1901, 1909), when he stated *Semudobia* to be responsible for deformations of male birch catkins! These deformations are not rare indeed and most causes were listed by Gäbler (1958). The deformations of female catkins, attributed to *Semudobia* by Swanton (1912), are doubtful too. Rübsaamen & Hedicke (1925—1939) figured the three different gall types (pl. XXV figs. 1—4) but again considered them to belong to one gall midge species. The only authors, who realized the different gall forms in female birch catkins to be due to different species, were Skuhravá & Skuhravý (1960, 1963).

Besides the gall inducing midges belonging to the genus *Semudobia* other gall midges, inquilines, and phytosaprophagous midges may be found in the fruit catkins of *Betula*. At least two, not identified, species of inquiline gall midges are common in the galled catkins and may occasionally pupate "in the interstices between the scales". So it seems probable that these inquilines were observed by Kaltenbach (1874) and Binnie (1877). Suggestions about the identity of these larvae were discussed later by Thomas (1893), Escherich (1942) and Skuhravá & Skuhravý (1963). Hodges (1969) reported *Clinodiplosis* sp. as an inquiline midge. Larvae of this genus are indeed frequent inhabitants of fruit catkins of *Betula*, but there is no correlation between the occurrence of this midge and the presence of *Semudobia* galls. *Clinodiplosis* is common in the "deformed and dwarfed catkins" described by Swanton (1912) and is supposed to be a fungus eater in these catkins (Skuhravá, 1970).

Larval characters. — Papillae of *Semudobia* larvae were studied by Rübsaamen (1892), Kieffer (1895) and Möhn (1955). Phase-contrast microscopy being unknown or uncommon in those days, it is not surprising that their data are very incomplete and not suitable to distinguish the species. About the spatula

sternalis, the characteristic chitinized structure on the ventral side of the third instar, more information can be found in the literature. Some variation is apparent. Kieffer (1913b) described a wide structure: "spatule sessile, large, partie basale presque transversale, partie antérieure moins large et bilobée". Rübsaamen & Hedicke (1925—39) depicted a small and oblong one. Möhn (1955) depicted a large and wide spathula. The description, given by Rübsaamen (1891), is remarkable. He described a small, short, bilobed structure, "an dieser Platte scheinen sich zwischen den beiden Lappen noch einige Zähne zu befinden". These small teeth were never reported again until Skuhravá & Skuhravý (1960) depicted the spathula. They noted that this particular form of spathula only will be found on larvae (Itonidae sp. in their terminology) living in galls that are coalescent with the spindle of the fruit catkin. They also depicted the two spathula types of *Semudobia* larvae living in fruit galls (in the strict sense), but supposed these to be examples of intraspecific variation.

A short note on phenology. — Many authors indicated the end of March until the beginning of May as the time of emergence of the adults. Forsius (1927), who reported *Semudobia* from Finland, reared adults in August (probably under unnatural conditions, as there are no receptive catkins at that time). This will be discussed below (vide Phenology, pag. 180).

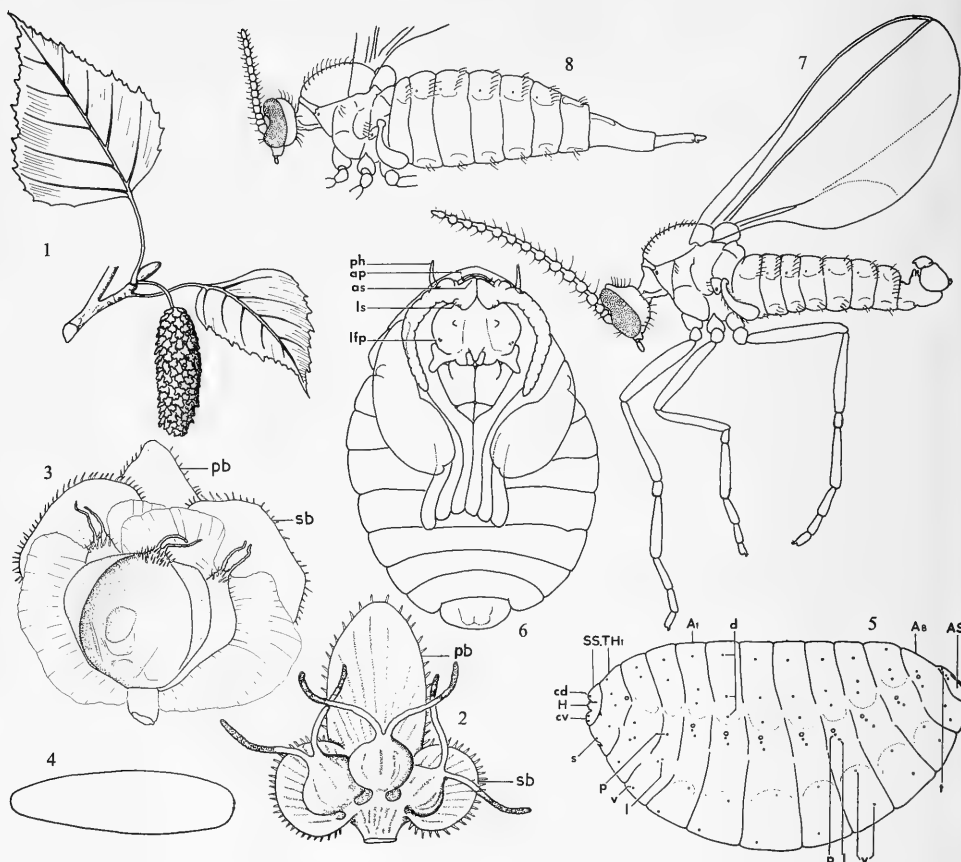
Other references of *Semudobia*. — Macquart (1853), Walker (1856), Döbner (1858), Schiner (1864), Von Bergenstamm & Löw (1876), Inchbald (1885), Lintner (1887), Liebel (1889), Rübsaamen (1892), Von Tubeuf (1893), Collin (1904), Houard (1908—13), Felt (1908, 1915, 1940), Küster (1911), Ross & Hedicke (1927), Docters van Leeuwen (1957), Gäbler (1958), Buhr (1964), Mamaev & Krivosheina (1965), Skuhravá & Skuhravý (1963), Bachmaier (1965), Gagné (1967).

Conclusion. — Differences in gall form (Rübsaamen & Hedicke, 1925—39) and the larval spathula (Skuhravá & Skuhravý, 1960, 1963) have already been recorded. These differences do not represent a range of intraspecific variation. After a careful analysis of material from all over the northern hemisphere, these differences are found to be supported by other characters concerning egg size, papillary pattern in larval and pupal stages, number and form of antennal segments, structure of genitalia and host parasite relations. Thus, it may be concluded that they are differential characters, on which the genus *Semudobia* may be divided into five species.

## MORPHOLOGY

The gall (fig. 3).

Inflorescences of birches (*Betula*, Betulaceae) are monoecious. The female birch catkin (fig. 1) consists of an elongated spindle bearing spirally arranged condensed dichasia (Porter, 1967). In each dichasium a leaf-like scale bears three axillary female flowers; the fruits are winged nutlets. In this paper, for convenience' sake, the scale is called "bract". This is not quite correct, because in the morphological sense it is a combination of a primary and two secondary bracts (fig. 2). Galling of tissues in the female catkin is exclusively the result of *Semudobia*



Figs. 1—8. Life cycle of *Semudobia*. 1, fruit catkin of *Betula*; 2, scale with female flowers; 3, scale with fruits, the middle one infected; 4, egg; 5, larva; 6, pupa; 7, male; 8, female. A1—A8, abdominal segments; AS, anal segment; H, head; SS, supernumerary segment; TH1, first thoracic segment; ap, apical papilla; as, apical spine; cd, dorsal collar papilla; cv, ventral collar papilla; d, dorsal papilla; l, lateral papilla; lfp, lateral facial papilla; ls, lateral spine; p, pleural papilla; pb, primary bract; ph, prothoracic horn; s, sternal papilla; sb, secondary bract; t, terminal papilla; v, ventral papilla. 3,  $\times 7$ ; 4,  $\times 100$ ; 5, 6,  $\times 35$ ; 7, 8,  $\times 25$ . 1, 2, after Strassburger et al., 1971.

activities. *Semudobia* galls are never observed outside female birch catkins. Galls may be found when infected catkins are sifted out by separating bracts and nutlets.

Eggs are deposited between the bracts and flowers. Gall forming is induced by the newly hatched larvae, which select the tissue to be infected. The different species prefer different tissues and this results in different gall forms. Detailed information about these forms will be given in the descriptions of the species.

As a rule, only one individual infects one bract or one ovary. Sometimes however, several (up to five!) individuals, which may belong to different species, are found in one single fruitlet. When not attacked by other insects, all these larvae will develop into normal adults. About at the beginning of the second instar a characteristic window-like spot (fig. 97) in the galled fruit is formed by

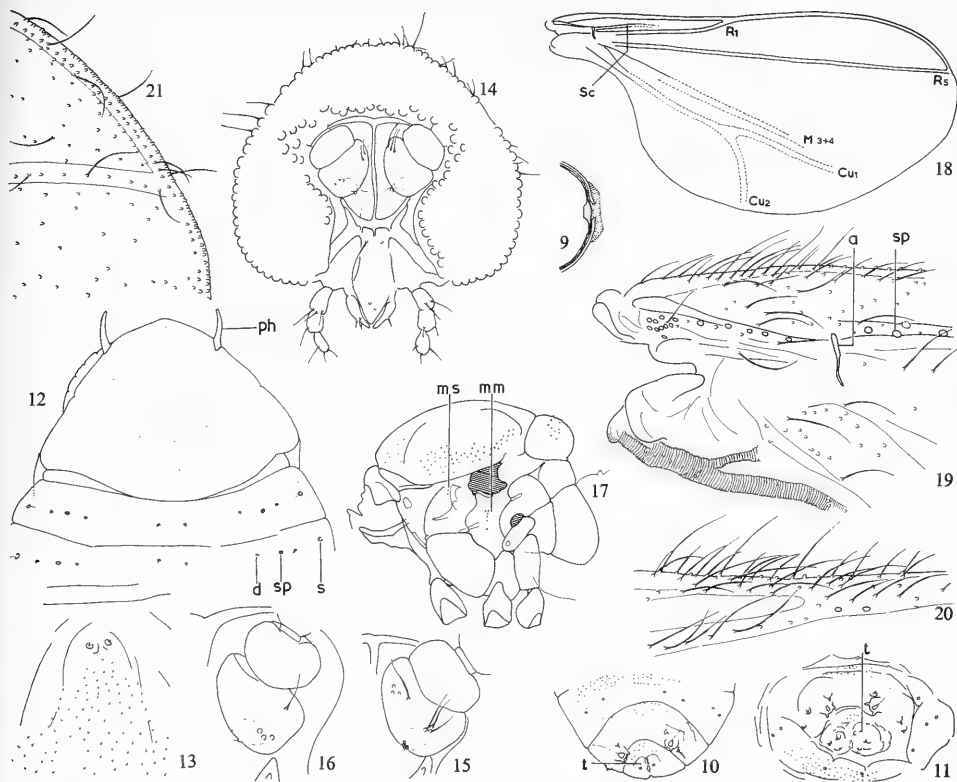


Fig. 9. Egg of *S. tarda*, detail of micropyle; 10—11, anal segment of first instar larva: 10, *S. betulae*, 11, *S. skuhravae*; 12—13, pupa of *S. skuhravae*: 12, dorsal aspect of thorax, 13, anterior ventral papillae on 7th abdominal segment; 14, *S. betulae*, ♂, head; 15—16, ♂, antennal scape: 15, *S. betulae*, 16, *S. brevipalpis*; 17, thorax of *S. betulae*, ♂, lateral aspect; 18—21, wing of *S. betulae*, ♂: 18, venation, 19, detail of base, 20, sensory-pores on distal part of R1, 21, detail of tip. a, arculus; d, dorsal papilla; mm, mesanepimeron; ms, mesanepisternum; ph, prothoracic horn; s, stigma; sp, sensory-pore; t, terminal papilla. 9—11,  $\times 325$ ; 12,  $\times 40$ ; 13,  $\times 250$ ; 14,  $\times 105$ ; 15—16, 19—21,  $\times 165$ ; 17—18,  $\times 35$ .

some of the species. This window functions as a "weak spot", through which the adults emerge. Some authors (Kieffer, 1895; Pitcher, 1957 and Hodges, 1969) supposed the window to be made by the larval spathula. This can not be correct in this case, because the spathula is only present in the third instar larva.

#### The egg (fig. 4).

Eggs may be found in the flowering female catkins of birch; they are scattered between the bracts and flowers. For detailed information about oviposition, see Hodges (1969). Freshly laid eggs are transparent, becoming orange-reddish when the larva develops. *Semudobia* eggs are centrolecital, the chorion is smooth and one micropyle is visible on the side where in the ripe egg the anal segment of the embryo will be situated (fig. 9). Egg sizes are taken of ovarian eggs and statistically more or less different egg sizes are found for the individual species (fig. 22). Per

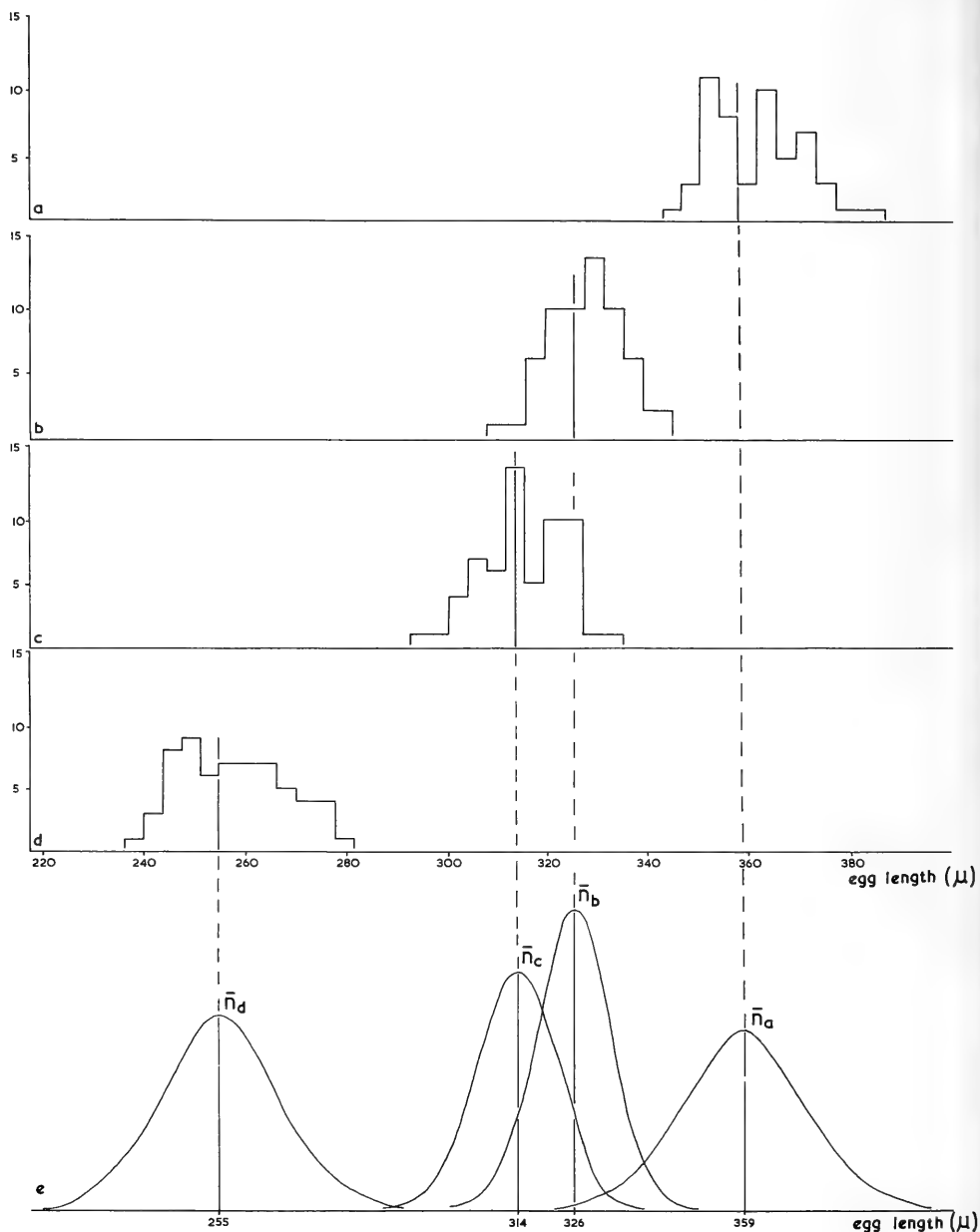


Fig. 22. Egg lengths of *Semudobia*. a—d, histograms: a, *S. skuhravae*, b, *S. betulae*, c, *S. brevipalpis*, d, *S. tarda*; e, corresponding frequency distributions.  $\bar{n}_a$ , mean value of *S. skuhravae*,  $\bar{n}_b$  of *S. betulae*,  $\bar{n}_c$  of *S. brevipalpis*,  $\bar{n}_d$  of *S. tarda* (*S. steenisi* not studied).

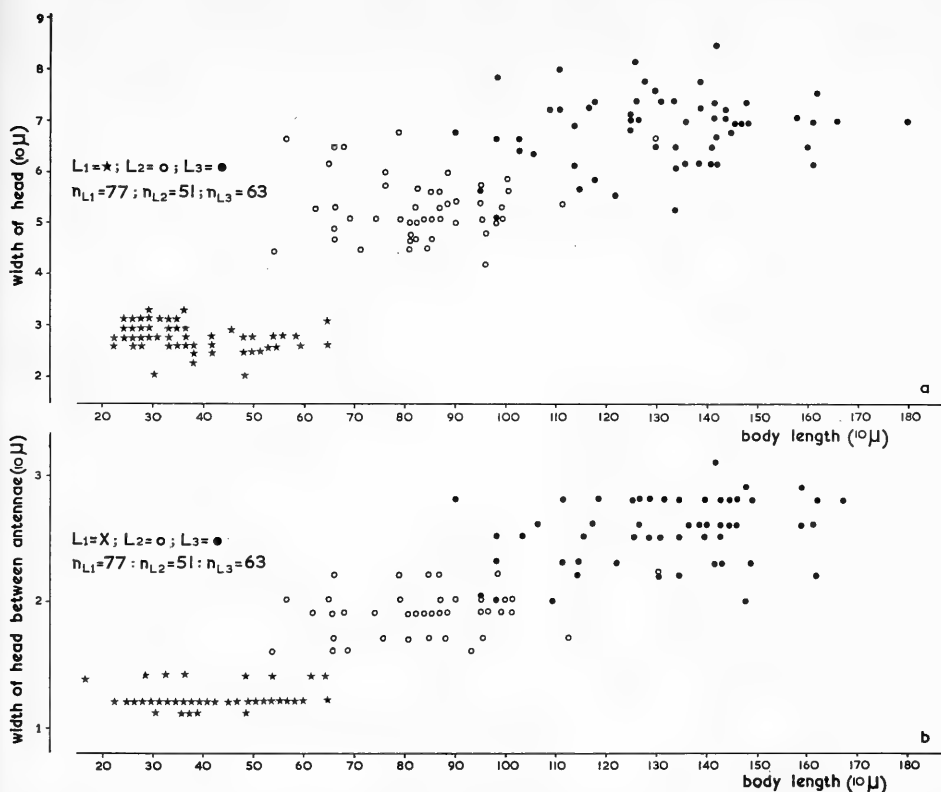


Fig. 23. The relation between body length and width of head (a), respectively width of head between antennae (b) for each of the three larval instars of *S. betulae*.

female five eggs are measured; four females are taken per population and three populations per species.

The larva (fig. 5).

Characters of all larval stages are of great value in gall midge systematics on the generic level. Moreover, they prove to be essential for the delimitation of the species of *Semudobia*. *Semudobia* midges pass through three larval stages. In all instars the larva consists of a weakly sclerotized head (H), a supernumerary segment (SS), three thoracic segments (Th 1—3) and nine abdominal segments, the last of which is the aral one (A 1—8, AS). From the dorsal side of the head-capsule arises a pair of short antennae. On the ventral side of the antennae a small, oval area is visible. The length of the antenna does not differ remarkably among the different species; it is  $2\mu$  in the first instar,  $6\mu$  in the second and  $11\mu$  in the third. Eye-spots are distinct in all stages, but not in the last inactive period of the third instar in which diapause is passed. In this full-grown larva the head is retracted into the supernumerary segment. Measurements of the head-capsule are given in the descriptions. As demonstrated in fig. 23, there is no correlation

between length and width of the capsule in any instar. An interstadial growth (as was found by Den Hollander, 1975, for *Tipula*) does not occur in larvae of these midges. *Semudobia* larvae are apodous. The colour of the first instar larva is pale orange, with a bright red spot where the mid gut is situated. There are 9–10 pairs of caeca. The second instar larva is yellowish pale orange and the third instar bright orange; when full-grown, it has a reddish tinged thorax.

Respiration in the first instar is, depending on the species, apneustic or metapneustic; when stigmata are developed, they are situated on A 8. In second and third instar larvae respiration is peripneustic; nine pairs of stigmata are developed on Th 1 and A 1–8.

Papillae are developed in a very definite pattern, that is the same for all instars but different for the various species. The terminology of Möhn (1955) is followed. Papillae are very distinct in the first larval stage. In that stage, only the dorsal, pleural and lateral papillae of A 8 and the terminal papillae of AS have a short seta (up to 1  $\mu$ ). In the second and third instars, however, usually all papillae have a short seta ( $\sim 2 \mu$ ). The papillary pattern of the head appears to be very complex and is not dealt with in this study. Depending on the species, the supernumerary segment may bear one pair of dorsal collar papillae (CD) and/or one or two pairs of ventral collar papillae (CV). On the dorsal surface of the thoracic segments, one or two pairs of rows of dorsal papillae (D) are developed, laterally there are two pairs of rows of pleural (P) and one or two pairs of rows of lateral papillae (L, subventral in position). On the ventral surface of Th 1 one pair of sternal papillae (S) is always distinct. The segments Th 2, 3 possess one pair of ventral papillae (V).

	THORAX										ABDOMEN							
	H	SS	TH <sub>1</sub>	2	3	A	1	2	3	4	5	6	7	8	AS			
a			D 2P L S	D 2P L V	D 2P L V	O	D P L V	O	D P L V	O	D P L V	O	D P L V	O	D P L V	O	D P L V	T
b			D 2P (2)L S	D 2P (2)L V	D 2P (2)L V	O	2D P L V	O	2D P L V	O	2D P L V	O	2D P L V	O	2D P L V	O	D P L V	T
c			D 2P 2L S	D 2P 2L V	D 2P 2L V	O	2D P L V	O	2D P L V	O	2D P L V	O	2D P L V	O	2D P L V	O	D P L V	2-3 T
d			D 2P L S	D 2P L V	D 2P L V	O	2D P L 2V	O	2D P L 2V	O	2D P L 2V	O	2D P L 2V	O	2D P L 2V	O	D P L 2V	2-3 T
e			2D (2)L S	2D 2P 2L V	2D 2P 2L V	O	3D P L 2V	O	3D P L 2V	O	3D P L 2V	O	3D P L 2V	O	3D P L 2V	O	D P L 2V	2-3 T

Fig. 24. Diagram of papillary pattern and tracheal system of third instar larvae, lateral aspect. a, *S. tarda*; *S. betulae*; c, *S. brevipalpis*; d, *S. steenisi*; e, *S. skuhravae*. A1–8, abdominal segments; AS, anal segment; CD, dorsal collar papilla; CV, ventral collar papilla; D, dorsal papilla; H, head; L, lateral papilla; P, pleural papilla; S, sternal papilla; SS, supernumerary segment; T, terminal papilla; TH1–3, thoracic segments; V, ventral papilla; O, stigma.



The dorsal surface of the abdominal segments A 1—7 offers the best diagnostic characters in papillary pattern. Depending on the species, 1—3 pairs of rows of dorsal papillae may be developed. Laterally one pair of rows of pleural papillae and one pair of rows of laterals can be observed. On the ventral surface of the segments A 1—7 there may be one pair of anterior papillae and/or one pair of posterior papillae. The anterior ventral papillae are in most species only visible in the young first instar. The A 8 segment has a more simple pattern. One pair of dorsal papillae is present in all species except one, in another species there are usually no lateral papillae. In general, one pair of both pleural and ventral papillae are present. Depending on the species, 1—3 pairs of papillae are present on the anal segment. In second and third instar larvae papillae are situated outside the anal field (a distinct area around the anus); these may be distinguished as terminal papillae (t, fig. 85). In the first instar larva, where the delimitation of the anal field is not clear (fig. 10, 11), the discrimination between anal and terminal papillae may be a moot point. Contrary to Möhn (1955), Hodges (1969) considered a papilla a simple skin-structure and not a sense-organ. The statements by Kieffer (1895) and Möhn (1955) that pleural papillae are not developed in *Semudobia* must be imputed to the less sophisticated microscopy techniques of that time. Papillary patterns are scheduled in fig. 24.

Skin structures, such as well developed spinule rows, are visible on the ventral and dorsal surfaces of the first instar larvae. On the dorsal surface of second instar larvae spinule rows may be less distinct. In regard to spinule rows it is possible to divide larval segments in an anterior and a posterior part. In the anterior part, the spinule rows are always distinct and they lie close to each other; in the posterior part, however, they lie further apart or, more often, are absent. The spinule rows are counted and the numbers are given in the descriptions. The first number concerns the posterior part of Th 3, the second relates to the anterior part of A 1. Between brackets the variation in number is given usually for ten specimens. Skin structures and papillae are distinct in newly hatched first instar or just moulted second instar larvae, but they become less distinct in older first and second stages. The third instar larva has a verrucose surface. Dorsally there are no remarkable differentiations, but ventrally the verrucae unite to form striae, while laterally they tend to be isolated and more rounded. In the figs. 72, 73, e.g., small fields are indicated that have no verrucose sculpture. On the ventral surface of the third instar prothorax (Th 1) lies a heavily chitinized structure: the spathula sternalis. Shape and size of the spathula, as suggested earlier, give good characters for the delimitation of the species.

When full-grown (about mid August, in The Netherlands), the larva produces a whitish membranous cocoon (see also Hodges, 1969) and is ready to hibernate.

The pupa (fig. 6).

In morphology and descriptions of the pupal stage mainly Möhn (1961) is followed. The colour of the pupa is bright orange. On the head, near the place where the adult pedicel will develop, two heavily chitinized blunt apical spines are formed. These spines help the pupa to perforate the window-pit of the gall just

before the adult emerges. Next to the apical spines two subrotund laterals are visible. Frontal spines are absent, on the ventro-lateral part of the future adult eye, one or two pairs of papillae are situated. Just caudal of the apical spines, a pair of slender apical papillae is present. From the dorsal side of the prothorax a pair of stout prothoracic horns (fig. 12) arises, on the end of which the prothoracic stigmata are located. The papillary pattern on the abdominal segments A 1—8 is in conformance with those of the larval stages and here also offer the best diagnostic characters. In the pupa, the anterior ventral papillae are often distinct (fig. 13). On the dorsal surface of A 1—7 a pair of rows of sensory-pores is also formed (fig. 12). The abdomen is covered with tiny, pointed setulae (fig. 13).

#### The adult.

In the descriptions of the adult stage mainly Harris (1966, 1968) is followed. For further details, see Gagné (1968, 1973) and Yukawa (1971), from whom some of the terms used are borrowed.

Male (fig. 7). — Body reddish-orange, with dark brown sclerotized parts. Eyes holoptic (fig. 14), with a slight, incomplete, median incision. Antenna with scape, pedicel and, depending on the species, 12—14 flagellomeres. The distal flagellomeres are often fused. If the last flagellomere is more than  $1\frac{1}{2}$  times the length of the penultimate one, the total count of flagellomeres is given as "n+" in the descriptions, rather than "n". Flagellomeres uninodal with subquadrate internodes (stalks); sensorial spines present, usually two per flagellomere and situated on antero-distal portion (fig. 33); circumfila simple, not looped; basal setae on horse-shoe-shaped sockets. Scape larger than pedicel, with a ventral area with very short setae and laterally and distally fields with long setae (fig. 15). Maxillary palpi three segmented.

Numbers of setae on mesanepisternum and mesanepimeron (fig. 17) are given in the descriptions. Sc of wing usually incomplete or absent, and indicated only by a number of sensory-pores (fig. 19); R5 well separated from R1, and joining C near wing apex. Cu halfway forked in Cu1 and Cu2; m 3 + 4, Cu1 and Cu2 only indicated as wing-folds; Rs absent. Tarsal claws simple, bent nearly at right-angle and a little shorter than empodia.

Abdominal terga 2—7 not strongly sclerotized, caudal row of setae present, basal row absent, only one pair of short setae cephalad of caudal row; sterna 2—7 with both basal and caudal rows of setae, one pair of median short setae cephalad of the basal row. Basimere (fig. 46) of genitalia stout with in internal angle a large claspette (mesolobe); distimere stout, in some species a little inflated, about half as long as basimere and with a dense row of strong teeth distally; superior lamella (tergum 10) with V-shaped incision, forming a pair of lobes which are rounded distally; inferior lamella (sternum 10) narrower than superior lamella and, depending on the species, shallowly emarginated to with V-shaped incision; aedeagus rather thick, distinctly shorter to a little longer than claspette.

Female (fig. 8). — Antenna with scape, pedicel and 11—13 subsessile flagellomeres. Ovipositor retractile, tapering to a simple upper lamella and a short to very short lower lamella (fig. 56, 57).

## METHODS

Measurements of galls are taken in dry condition; in the case of fruit galls stigmata and wings are excluded. Sizes of galls given are only valid for the host plant species mentioned in the descriptions and for the galls inhabited by one gall midge only.

Eggs are dissected from identified females and macerated in warm (85-90°C) 80% lactic acid. After being straightened under a cover-slip, length and width are measured in the same medium. Midges, from which ovarian eggs are taken, are preserved on a 70 : 15 : 15% aethanol-glycerol-water mixture. Eggs of females preserved in other ways may not give comparable results.

Preparation of the larvae, especially of first and second stages, may cause many difficulties. Therefore rather detailed information is given here about techniques. Newly hatched larvae are collected from catkins just after flowering. These catkins are freshly deep-frozen or preserved on a 70 : 15 : 15% mixture of aethanol-glycerol-water. Older larvae are dissected from fresh or dried (herbarium specimens) galls and preserved either dry, or in the same aethanol-glycerol-water mixture. Fresh larvae are macerated in warm 80% lactic acid. Larvae from dried galls first have to be hydrated carefully in a series of 90, 70, 30% solutions of aethanol and in water before maceration in 80% lactic acid is possible. Swelling of the body content, which might result in total distortion of the larval skin, is thus prevented. Small larvae, first instar and young second instar, are examined in the maceration medium. For a slide collection these larvae are mounted in polyvinyl-lactophenol (Chroma Gesellschaft Schmid & Co., Stuttgart, Germany). To avoid shrinking, the very tender skins are transferred to the mounting medium without neutralizing or rinsing. The older larvae are washed in water after maceration and the residuals of body contents are very carefully removed. The macerated larvae are stored and examined in glycerol.

Pupae are dissected from the galls and macerated in 80% lactic acid. After rinsing the pupae have to pass a series of 30, 70, 96% aethanol before being mounted in euparal.

Measurements of all immature stages are taken from specimens straightened under a cover-slip.

To rear the adults, galls are sorted according to the identification key for the galls on page 166. The samples, mixed with peat-litter and deposited in glass-vials, are allowed to pass diapause under more or less natural conditions. From January on, the glass vials are transmitted to sand-filled flowerpots and kept in a climate chamber (20° C, long day light regime). The cultures are moistened with 1% propionic acid to prevent damage by mould infections. After emergence the adults are promptly killed in a mixture of 70 : 15 : 15% aethanol-glycerol-water and stored in the same medium. Because maceration might disturb tiny organs as antennae, the specimens are directly dehydrated in a series of 30, 70, 96% aethanol. After clearing in oil of cloves the specimens are mounted in euparal. On the slide the head, left wing and male genitalia are mounted under separate cover-slips. The body is slide-mounted in a lateral position, the head with the face up, the genitalia dorsal surface up.

For examination a phase-contrast microscope (Zeiss, objectives Ph 10, 25, 40 and 63  $\times$ ) is used.

## TAXONOMIC PART

### *Semudobia* Kieffer

*Cecidomyia* Meigen (partim); Winnertz, 1853: 234.

*Hormomyia* Rübsaamen, 1891: 137.

*Oligotrophus* Latreille (partim); Kieffer, 1900: 22.

*Semudobia* Kieffer, 1913a: 55.

Type-species: *Cecidomyia betulae* Winnertz, 1853:234.

### Keys to species of *Semudobia*

(Egg sizes are not used in the keys because their accurate analysis was only performed in the ovarian stage; fig. 22.)

#### Males

1. Third palp segment shorter than the second; claspettes rectangular, distally emarginated; mainly Palaearctic species . . . . . *tarda* sp. n.
- Third palp segment longer than the second; claspettes more or less triangular, never distally emarginated . . . . . 2
2. Ultimate flagellomere rather rounded, internodes transverse to subquadrate; first and second palpal segments not broadly fused; claspettes verrucose; aedeagus usually a little shorter than claspettes . . . . . *skuhravae* sp. n.
- Ultimate flagellomere rather pointed, internodes oblong; first and second palpal segment broadly fused; surface of claspettes only finely sculptured; aedeagus always a little longer than claspettes . . . . . 3
3. Antenna with 14 flagellomeres, at least 3 times the width of the head; internode of third flagellomere at least 0.5 times the length of the node of this segment; West-Nearctic species . . . . . *steenisi* sp. n.
- Number of flagellomeres less than 14, length of antenna never more than 2.6 times the width of the head . . . . . 4
4. Never more than one seta on distal surface of scape and then laterally placed (fig. 16); third palpal segment at least 1.7 times the length of the second; at least 5 setae on mesanepisternum and 8 on mesanepimeron; inferior lamella about half-way with U-shaped incision, lobes acute; East-Nearctic species . . . . . *brevipalpis* sp. n.
- 3—10 setae on distal surface of scape (fig. 15); length of third palpal segment not more than 1.4 times the length of the second; not more than 3 setae on mesanepisternum and not more than 5 on mesanepimeron; inferior lamella not more than for about one-third V-shapedly incised, lobes rounded; mainly Palaearctic species . . . . . *betulae* Wtz.

## Females

1. Tergum 8 triangular, length of this sclerite about equal to its width; ovipositor always longer than hind femur, with heavily chitinized vaginal furca; inferior lamella very short and truncate; mainly Palaearctic species . . . . . *tarda* sp. n.
- Tergum 8 sub-triangular or rectangular to H-shaped, always somewhat longer than wide; ovipositor shorter than hind femur; vaginal furca not remarkably chitinized; inferior lamella at least a little shorter than wide, rounded . . . . . 2
2. Ultimate flagellomere rounded; first and second palpal segments never broadly fused . . . . . *skuhravae* sp. n.
- Ultimate flagellomere pointed; first and second palpal segments broadly fused . . . . . 3
3. Antenna at least two times the width of the head; West-Nearctic species . . . . . *steenisi* sp. n.
- Antenna never more than two times the width of the head . . . . . 4
4. Distal setae on scape, when present, then placed laterally; third palpal segment at least 1.5 times the length of the second, length of tergum 8 never more than 1.5 times its width; length of superior lamella about 1.3 times its height; East-Nearctic species . . . . . *brevipalpis* sp. n.
- Distal setae on scape, when present, never placed laterally; third palpal segment never more than 1.5 times the length of the second; length of tergum 8 about two times its width; length of superior lamella at least two times its height; mainly Palaearctic species . . . . . *betulae* Wtz.

First instar larvae<sup>1)</sup>

(No stigmata, or only one pair of stigmata developed, spathula sternalis absent.)

1. No stigmata developed at all; only one pair of rows of dorsal papillae on abdominal segments A 1—7, no dorsal papillae on A 8 (the penultimate body segment) . . . . . *tarda* sp. n.
- One pair of stigmata on A 8; at least two pairs of rows of dorsal papillae on segments A 1—7, one pair on A 8 . . . . . 2
2. Three pairs of rows of dorsal papillae on A 1—7, one pair of dorsal collar papillae, on A 8 pleural and lateral papillae both developed . . . . . *skuhravae* sp. n.
- Two pairs of rows of dorsal papillae on A 1—7, no dorsal collar papillae, on A 8 no lateral papillae developed . . . . . *betulae* Wtz.

## Second instar larvae

(Stigmata developed on first thoracic segment and first to eighth abdominal segments; no spathula sternalis. Same key as for third instar, characters based on spathula excluded.)

<sup>1)</sup> Nearctic species not studied and therefore excluded from this key.

## Third instar larvae

(Nine pairs of stigmata (vide second instar) and spathula sternalis developed.)

1. Spathula sternalis with a variable number of smaller teeth (as if broken off) between the usually larger lobes; three pairs of rows of dorsal papillae on A 1—7 . . . . . *skuhravae* sp. n.
- Spathula always bilobed; only one or two pairs of rows of dorsal papillae on A 1—7 . . . . . 2
2. Spathula large, lobes at least 15  $\mu$  high; only one pair of rows of dorsal papillae on A 1—7 . . . . . *tarda* sp. n.
- Spathula smaller, height of lobes never more than 10  $\mu$ ; always two pairs of rows of dorsal papillae . . . . . 3
3. Spathula oblong, at least 50  $\mu$  high; no lateral papillae on A 8, only one pair of terminal papillae; mainly Palaearctic species . . . . . *betulae* Wtz.
- Spathula subquadrate to transverse, never more than 50  $\mu$  high; lateral papillae on A 8 present, 2—3 pairs of terminal papillae . . . . . 4
4. Lobes of spathula at least 5  $\mu$  high, one pair of rows of lateral papillae on thoracic segments, two pairs of rows of ventrals on segments A 1—7; West-Nearctic species . . . . . *steenisi* sp. n.
- Lobes of spathula never more than 5  $\mu$  high, two pairs of rows of lateral papillae on thoracic segments, one pair of rows of ventrals on segments A 1—7; East-Nearctic species . . . . . *brevipalpis* sp. n.

Pupae<sup>1)</sup>

1. Two pairs of rows of dorsal papillae, dorsally of sensory-pores, on abdominal segments A 1—7 . . . . . *skuhravae* sp. n.
- Only one pair of rows of dorsal papillae, dorsally of sensory-pores, on A 1—7 . . . . . 2
2. No dorsal papillae laterally of sensory-pores on A 1—7, dorsal papillae on A 8 absent . . . . . *tarda* sp. n.
- One row of dorsal papillae laterally of sensory-pores on A 1—7, one pair of dorsal papillae on A 8 . . . . . 3
3. Prothoracic horn longer than 120  $\mu$ , about 0.08 times the body-length or more; mainly Palaearctic species . . . . . *betulae* Wtz.
- Prothoracic horn shorter than 100  $\mu$ , about 0.06 times the body-length or less; West-Nearctic species . . . . . *steenisi* sp. n.

## Galls

1. Either the axil of the scale is galled, or the galled fruit is distinctly coalescent with the scale; window-pit absent . . . . . *skuhravae* sp. n.
- Galling of the fruit, the gall is in ripe situation never coalescent with the scale . . . . . 2
2. Window-pit absent or indistinct, gall subrotund and glabrous, wings of fruit often completely reduced . . . . . *tarda* sp. n.

<sup>1)</sup> *S. brevipalpis* not studied and therefore excluded from this key.

- Window-pit(s) distinct . . . . . 3
- 3. Often a window-pit on both sides of the gall, one of them large; gall glabrous, wings of fruit often completely reduced; East-Nearctic species *brevipalpis* sp. n.
- Only one window-pit developed; gall more or less hairy, wings present . . . 4
- 4. Gall usually concave on ad-axial side, window-pit irregularly formed; West-Nearctic species . . . . . *steenisi* sp. n.
- Gall usually convex on both sides, window-pit subrotund; mainly Palearctic species . . . . . *betulae* Wtz.

### **Semudobia betulae (Winnertz)**

(male: figs. 14, 15, 17—21, 32, 33, 42, 43; female: figs. 40, 41, 50, 54, 55, 102; imm. stages: figs. 10, 64, 65, 70—75, 95—97)

Male. — Width of head 1.17 (1.12—1.30) times its height. Antenna (figs. 32, 33) with 2 + 12 segments, its length 2.53 (2.49—2.60) times the width of head; scape ventrally with 2 (2—4) very short, 4 (3—4) lateral and 10 (3—10) dorsal long setae; third flagellomere with its node 1.07 (1.00—1.08) times as long as its diameter; internodes oblong, internode of third flagellomere 0.48 (0.38—0.48) times as long as node. Maxillary palp 0.24 (0.24—0.28) times the width of head; third segment 1.27 (1.14—1.38) times as long as the second; first and second segments partially grown together. Fronto-clypeal setae 7 (2—7); 2 (2—3) setae on mesanepisternum, 5 (4—6) on mesanepimeron. Wing length 1.68 (1.56—1.74) mm, 2.0 (1.9—2.2) times as long as wide; R5 2.3 (2.2—2.3) times as long as R1; Sc indicated by 4 (3—4) sensory-pores, 4 (3—5) sensory-pores on basal part of R1 and 2 on distal part, 3 pores on medio-distal portion of R5. Tibia of hind leg 0.94 (0.78—0.98) times as long as femur, second tarsal segment 0.54 (0.46—0.57) times this length; fifth tarsal segment 0.85 (0.83—0.85) times as long as the fourth. Distimere (fig. 42) 0.47 (0.47—0.58) times as long as basimere; inferior lamella weakly emarginate to incised for about one-third, the incision broadly V-shaped, its sides converging to its apex (fig. 43); aedeagus a little longer than the usually weakly chitinized, rounded triangular claspettes.

Female. — Width of head 1.15 (1.15—1.28) times its height. Antenna (figs. 40, 41) with 2 + 11+ (10+—12) segments, its length 2.00 (1.44—2.00) times the width of head; scape ventrally with 3 (2—3) very short, 3 (2—3) lateral and 3 (0—3) dorsal long setae; third flagellomere with its node 1.08 (1.04—1.09) times as long as its diameter. Maxillary palp (fig. 102) 0.28 (0.24—0.30) times the width of the head; length of third segment 1.46 (1.25—1.46) times the length of the second; first and second segments partially grown together. Fronto-clypeal setae 10 (1—10); 3 (2—3) setae on mesanepisternum, 7 (5—7) setae on mesanepimeron. Wing length 2.00 (1.66—2.14) mm, 2.1 (2.0—2.1) times as long as wide; R5 2.4 (2.3—2.4) times as long as R1; Sc indicated by 5 sensory-pores, 6 (4—6) sensory-pores on basal part of R1 and 2 on distal part, 3 on medio-distal portion of R5. Tibia of hind leg 0.89 (0.88—0.90) times as long as femur, second tarsal segment 0.43 (0.41—0.46) times this length; fifth tarsal segment 0.86 (0.83—0.92) times as long as the fourth. Tergum 8 subtriangular (fig. 50), the height of this sclerite about 2 times its width. Ovipositor (fig. 55) 0.75 (0.75—0.87) times as long as hind femur, for one- to about

three-quarters retracted into the eighth abdominal segment; vaginal furca not remarkably chitinized; superior lamella 2.5 (2.3—3.0) times as long as high; inferior lamella with a length about equal to its width (fig. 54).

Immature stages. — Egg length  $\bar{n}$  326  $\mu$ ,  $\bar{n} \pm 2$  SD. (95% of egg lengths) between 312—340  $\mu$ ; width  $\bar{n}$  106  $\mu$ . First instar larva (figs. 64, 65); length 255 (221—642), width 73 (73—339)  $\mu$ ; width of head-capsule 26 (21—47)  $\mu$ , between antennae 12 (11—14)  $\mu$ ,  $n = 76$ ; dorsal spinule-rows 4 (4—0) + 9 (7—10), ventrals 4 (4—0) + 8 (7—9),  $n = 10$ ; respiration metapneustic. Second instar (fig. 70); length 664 (537—1296), width 269 (269—664)  $\mu$ ; width of head-capsule 65 (45—68), between antennae 22 (16—22)  $\mu$ ,  $n = 50$ ; dorsal spinule-rows in posterior part absent, in anterior 4 (4—0), ventrals in posterior part absent either, in anterior part 8 (8—0),  $n = 10$ . Third instar (figs. 71—73); length 1422 (901—1801), width 948 (584—1138)  $\mu$ ; width of head-capsule 71 (45—85), between antennae 23 (17—31)  $\mu$ ,  $n = 63$ ; spathula sternalis bilobed (figs. 74, 75), width 24 (19—28), height 60 (52—64), distance between points of lobes 14 (13—22), height of lobes 9 (8—9), height of median incision 9 (5—9)  $\mu$ ,  $n = 10$ . Pupa length 1228 (1212—1643), prothoracic horns 126 (122—146), apical papillae 28 (28—43)  $\mu$ ,  $n = 8$ ; sensory-pores between the corresponding papillae of the two pairs of dorsal rows (fig. 95).

Papillary pattern (fig. 24b). Dorsal collar papillae absent, one pair of ventral collar papillae. On thoracic segments one pair of dorsal papillae, 2 pairs of pleural papillae and (one or) two pairs of laterals; on Th 1 one pair of sternal papillae, on Th 2 and 3 one pair of ventrals. On segments A 1—7 two pairs of dorsal papillae, one pair of pleurals and one pair of laterals, one (or two) pairs (posterior ventral papillae only distinct in first instar) of ventral papillae; on A 8 one pair of dorsal, pleural and ventral papillae, lateral papillae absent; one pair of terminal papillae on AS.

Gall (fig. 97) length 1.6—2.1 mm,  $\bar{n}$  1.8 mm, width 1.0—1.8 mm,  $\bar{n}$  1.3 mm,  $n = 20$ ; galling of the fruit; gall ovoid, more or less hairy, wings present, although not so large as in healthy fruits; window-pit distinct (*B. pubescens*).

Type material. — The type of *Cecidomyia betulae* Winnertz was destroyed in 1945 during the bombing of the Zoological Museum of Bonn (Möhn and Ulrich, in litt.), and no other specimens of the original series exist. In regard to the (wrong) low number of antennal segments in the original description, there is a good chance that the type-specimen Winnertz described, belonged to this species. The other species that could have been in Winnertz' material, all have more antennal segments. Moreover, in Poland, where the type-locality is situated, this species seems to be most common. A new type is selected: Neotype ♂, slide no. 760223.8, The Netherlands, Renkum, 15.i.1975, ex fruit galls of *B. pendula*, Allotype ♀, slide no. 760206.3, The Netherlands, Meyendel, 28.iv.1975, ex fruit galls of *B. pubescens*, leg. J. C. Roskam. Although this material does not originate from Poland, it comes as near to the original type locality as in my case is practicable (cf. Code, article 75 c5).

The original host-plant, *B. alba*, is a polytypic species, comprising among others *B. pendula* and *B. pubescens*. Paratypical material is presented to the Bonn Museum.



Material (all my localities are from The Netherlands) in coll. Rijksmuseum van Natuurlijke Historie, Leiden. Adults slides no. 760223.7—8, 760206.2—3, 760216.1, Renkum, 15.i.1975, ex fruit galls of *B. pendula* (♂); Meyendel, 28.iv.1975, ex fruit galls of *B. pubescens* (♀). First instar larva slide no. 750519.1, Duivenvoorde, 19.v.1975, ex *B. pubescens*; second instar slide no. 750619.4, Duivenvoorde, 19.vi.1975, ex fruit galls of *B. pubescens*; third instar slide no. 751001.1, Meyendel 1.x.1975, ex fruit galls of *B. pubescens*; pupa slides no. 730402.1—2, 730410.1—4, Meyendel, 2 and 10.iv.1973, ex fruit galls of *B. pendula*, leg. J. C. Roskam.

### ***Semudobia brevipalpis* sp. nov.**

(male: figs. 16, 30, 31, 44, 45; female: figs. 38, 39, 51, 56, 57, 103; imm. stages: figs. 77—81, 98)

Male. — Width of head 1.32 (1.25—1.32) times its height. Antenna (figs. 30, 31) with 2 + 13+ (12+—13+) segments, its length 2.45 (2.41—2.60) times the width of the head; scape ventrally with 1 (0—1) very short, 5 (4—5) lateral and 1 (0—1) latero-distal long setae; third flagellomere with its node 1.10 (1.04—1.15) times as long as its diameter; internodes oblong, internode of third flagellomere 0.42 (0.42—0.48) times as long as the node. Maxillary palp 0.19 (0.19—0.22) times the width of head; third segment 2.00 (1.73—2.20) times as long as the second; first and second segments partially grown together. Fronto-clypeal setae 2 (2—5), 12 (5—13) setae on mesanepisternum, 11 (8—11) on mesanepimeron. Wing length 1.78 (1.52—1.78) mm, 2.0 (2.0—2.1) times as long as wide; R5 2.2 (2.1—2.2) times as long as R1; Sc indicated by 4 (4—5) sensory-pores, 4 (4—6) pores on basal part and 3 (2—3) on distal part of R1, 3 sensory-pores on medio-distal portion of R5. Tibia of hind leg 0.76 (0.72—0.87) times as long femur, second tarsal segment 0.44 (0.43—0.50) times this length; fifth tarsal segment 0.85 (0.80—0.91) times as long as fourth. Distimere acute (fig. 44), 0.55 (0.45—0.56) times as long as basimere; inferior lamella about half way U-shapedly incised, sides converging to apex, lobes distally acute (fig. 45); aedeagus a little longer than the weakly chitinized, broadly rounded triangular claspettes.

Female. — Width of head 1.32 (1.31—1.34) times its height. Antenna (figs. 38, 39) with 2 + 11+ (10—12) segments, its length 1.61 (1.56—1.67) times the width of head; scape ventrally with 1 (0—1) very short, 4 (3—4) lateral and 1 (0—1) latero-distal long setae; third flagellomere with its node 1.09 (1.09—1.25) times as long as its diameter. Maxillary palp (fig. 103) 0.19 (0.19—0.24) times the width of head; length of third segment 2.00 (1.55—2.22) times the length of second; first and second segments partially grown together. Fronto-clypeal setae 2 (0—4), 4 (3—6) setae on mesanepisternum, 6 (3—14) setae on mesanepimeron. Wing length 1.68 (1.68—1.84) mm, 2.18 (2.17—2.31) times as long as wide; R5 2.22 (2.10—2.22) times as long as R1; Sc indicated by 4 (3—4) sensory-pores, 3 pores on basal and 2 (2—3) on distal part of R1, 3 on medio-distal portion of R5. Tibia of hind leg 0.83 (0.82—0.87) times as long as femur, second tarsal segment 0.46 (0.44—0.49) times this length; fifth tarsal segment 0.89 (0.82—0.91) times as long as fourth. Tergum 8 triangular (fig. 51), the height of this sclerite a little more than its width. Ovipositor (fig. 57) 0.71 (0.70—0.73) times as long as hind femur, for about the half retracted

into the eighth abdominal segment; vaginal furca not remarkably chitinized, superior lamella about a third longer than high, inferior lamella a little shorter than wide (fig. 56).

Immature stages. — Egg length  $\bar{n}$  314  $\mu$ ,  $\bar{n} \pm 2$  SD (95% of egg lengths) between 297—331  $\mu$ ; width  $\bar{n}$  112  $\mu$ . First, second instar larvae and pupae are not collected. Third instar (figs. 77—79): length 1388 (1101—1404), width 1069 (718—1084)  $\mu$ , width of head-capsule 79 (61—83), between antennae 24 (20—28)  $\mu$ ; spathula sternalis very wide with two small lobes (figs. 80, 81); width 55 (42—71), height 25 (16—28), distance between points of lobes 39 (28—52), height of lobes 3 (2—5), height of median incision 6 (5—8)  $\mu$ ,  $n = 15$ . Pupae not collected.

Papillary pattern (fig. 24c) very similar to *S. betulae*. Lateral papillae present on A 8, on AS 2—3 pairs of terminal papillae.

Gall (fig. 98) length 1.5—2.0 mm,  $\bar{n}$  1.8 mm, width 0.9—1.4 mm,  $\bar{n}$  1.2 mm,  $n = 20$ ; galling of the fruit, the gall is obovate and glabrous, wings almost completely reduced, window-pit distinct, usually developed on both ad- and abaxial side of the gall (*B. populifolia*).

Type material. — Holotype ♂, slide no. 760220.4, Allotype ♀, slide no. 760318.1. Canada, Quebec, natural forest along Trans-Canada Highway, 9.ii.1975, ex fruit galls of *B. papyrifera*, leg. W. F. Grant.

Material in coll. Rijksmuseum van Natuurlijke Historie, Leiden. Adults slides no. 760220.1, 3—4, 750209.10, 760213.1, 760218.2—3, same data as type material. Third instar larva slide no. 761101.14, same data as type-material.

The species is quite close to *S. betulae*: the larvae and pupae have two pairs of rows of dorsal papillae on the abdomen, also the adult antennae are quite similar. Nevertheless there are striking differences, viz., in the larvae the broad spathula with the very small lobes, in the adults the bristles in latero-distal position on the scape, the very short second palp segment, the broadly emarginated inferior lamella in the male and the short, plump superior lamella in the female genitalia.

### *Semudobia steenisi* sp. nov.

(male: figs. 109, 110, 113, 114; female: figs. 106—108, 111, 112, 115; imm. stages: figs. 116—122)

Male. — Width of head 1.12 (1.09—1.16) times its height. Antenna (figs. 109, 110) with 2 + 14 segments, its length 3.39 (3.18—3.97) times the width of head; scape ventrally with 4 (1—4) very short, 3 (3—4) lateral and no dorsal long setae; third flagellomere with its node 1.00 (1.00—1.06) times as long as its diameter; internodes oblong, internode of third flagellomere 0.63 (0.58—0.65) as long as the node. Maxillary palp 0.24 (0.22—0.28) times the width of head, third segment 1.20 (1.12—1.35) times as long as second; first and second segments partially grown together. Fronto-clypeal setae 2 (2—5); setae on mesanepisternum 1 (0—3), 2 (2—5) setae on mesanepimeron. Wing length 1.86 (1.64—1.91) mm, 2.29 (2.28—2.46) times as long as wide; R<sub>5</sub> 2.11 (1.88—2.17) times as long as R<sub>1</sub>; Sc indicated by 6 (4—7) sensory-pores, sensory-pores on basal part of R<sub>1</sub> indistinct and 2 on distal part, 3 pores on medio-distal portion of R<sub>5</sub>. Tibia of hind leg 0.79 (0.76—0.91) times as long as femur and second tarsal segment 0.59 (0.50—0.64) this length; fifth tarsal segment 0.62 (0.62—0.77) times as long as fourth. Distimere

(fig. 113) 0.46 (0.46—0.52) times as long as basimere; inferior lamella weakly emarginate (fig. 114); aedeagus about as long as the chitinized, triangular, rather slender claspettes.

Female. — Width of head 1.15 (1.12—1.15) times its height. Antenna (figs. 111, 112) with 2 + 12+ segments, its length 2.07 (2.03—2.33) times the width of head; scape ventrally with 2 (2—4) very short, 3 lateral and no dorsal long setae; third flagellomere with its node 1.06 (1.00—1.11) times as long as its diameter. Maxillary palp (fig. 115) 0.31 (0.28—0.32) times the width of the head; length of third segment 1.15 (1.06—1.20) times the length of the second; first and second segments partially grown together. Fronto-clypeal setae 3 (2—3); 3 (2—5) setae on mesanepisternum, 3 (2—4) setae on mesanepimeron. Wing length 1.86 (1.84—2.00) mm, 2.48 (2.31—2.48) times as long as wide; R5 2.11 (2.11—2.28) times as long as R1; Sc indicated by 4 (4—7) sensory-pores, 3—5 indistinct sensory-pores on basal part of R1 and 2 (2—3) on distal part, 3 pores on medio-distal portion of R5. Tibia of hind leg 0.79 (0.77—0.82) times as long as femur, second tarsal segment 0.63 (0.61—0.70) times this length; fifth tarsal segment 0.77 (0.77—0.87) times as long as fourth. Tergum 8 bluntly triangular to H-shaped (fig. 108), the height of this sclerite about one-and-a-half times its width. Ovipositor (fig. 106) 0.77 (0.72—0.81) times as long as hind femur, for one to about three-quarters retracted into the eighth abdominal segment; vaginal furca not remarkably chitinized; superior lamella 1.92 (1.71—1.92) times as long as high; inferior lamella a little shorter than wide (fig. 107).

Immature stages. — Egg length and first instar larvae not studied. Second instar (fig. 117) length 821, width 483  $\mu$ ; width of head-capsule 47, between antennae 17  $\mu$ ; dorsal spinule rows in posterior part absent, in anterior part 3; ventrals in posterior part absent too, in anterior part 7;  $n = 1$ . Third instar (figs. 118—120) length 1563 (1420—1723)  $\mu$ , width 1101 (909—1196)  $\mu$ ; width of head-capsule 57 (52—86), between antennae 30 (28—39)  $\mu$ , spathula sternalis (figs. 121, 122) bilobed, it may form one structure or consist of two independent pieces; width 31 (28—52), height 22 (19—42), distance between points of lobes 11 (11—39), height of lobes 6 (5—8), height of median incision 8 (6—9)  $\mu$ ,  $n = 16$ . Pupa length 1372 (1324—1627)  $\mu$ ; prothoracic horns 79 (71—94)  $\mu$ ; apical papillae 30 (25—36)  $\mu$ ;  $n = 4$ .

Papillary pattern (fig. 24d) rather similar to *S. betulae*. Only one pair of lateral papillae on thoracic segments and two pairs of ventrals on segments A 1—7; on AS 2—3 pairs of terminal papillae.

Gall (fig. 116) length 2.1—3.0 mm,  $\bar{n}$  2.6 mm, width 1.4—2.1 mm,  $\bar{n}$  1.8 mm,  $n = 20$ ; galling of the fruit; the gall is obovate and usually concave on ad-axial side, more or less hairy, wings present, although not so large as in healthy fruits; window-pit distinct (*B. occidentalis*).

Type material. — Holotype ♂, slide no. 761101.4, Allotype ♀, slide no. 761101.10. U.S.A., Wyoming, Fremont County, Wind River, 10 miles north of Dubois, 17.ix.1976, ex fruit galls of *B. occidentalis*, leg. J. C. Roskam.

Material in coll. Rijksmuseum van Natuurlijke Historie, Leiden. Adults slides no. 761101.1—3, 5—9, 11—12, same data as type-material. Second instar larva

slide no. 730411.3, Canada, Br. Columbia, O'Kanagan Valley, 13.viii.1959, ex fruit galls of *B. occidentalis*, leg. C. G. G. J. van Steenis; third instar slide no. 761101.13, same data as type material; pupa slide no. 730413.13, U.S.A., Montana, Bridger Cañon, alt. 1600 m, 16.ix.1905, ex fruit galls of *B. occidentalis*, leg. Blankinship 460.

I have great pleasure in naming this species after prof. dr. C. G. G. J. van Steenis, Rijksherbarium, Leiden. He collected the herbarium specimen of river birch in which I found larvae of this species. Together with *S. betulae* and *S. brevipalpis*, *S. steenisi* belongs to the "*betulae* species complex". All these species induce fruit galls with window-pits and have larvae with two pairs of rows of dorsal papillae on the A 1—7 segments. *S. steenisi* is the only species of this complex with only one pair of rows of lateral papillae on the thoracic segments and two pairs of rows of ventrals on the abdominal ones. The pupae have short prothoracic horns. Especially in the males the long antennae with very long internodes are remarkable; in females the length of the superior lamella of the ovipositor is just intermediate between *S. betulae* and *S. brevipalpis*.

Only at a very late moment during this study I recognised West-Nearctic midges of fruit galls to be different from East-Nearctic ones. Before my collection trip to the U.S.A. in 1976 I considered all the larvae derived from Nearctic fruit galls to belong to one, very variable, species. After this trip I reared adults of West-Nearctic material. These adults were different from East-Nearctic midges in many characters. Moreover, it was possible to correlate these differences with differences in larval characters. Because the plates of the other *Semudobia* species were completed before I depicted *S. steenisi*, all the figures of this species are united in the final two plates of this paper.

### ***Semudobia tarda* sp. nov.**

(male: figs. 28, 29, 46, 47; female: figs. 36, 37, 52, 58, 59, 104; imm. stages: figs. 9, 62, 63, 88—94, 99)

Male. — Width of head 1.23 (1.18—1.26) times its height. Antenna (figs. 28, 29) with 2 + 14 segments, its length 2.81 (2.65—2.81) times the width of head; scape ventrally with 3 (2—3) very short, 4 (3—4) lateral and 0 (0—6) dorsal long setae; third flagellomere with its node 1.11 (0.96—1.11) times as long as its diameter; internodes subquadrate to oblong, internode of third flagellomere 0.48 (0.46—0.56) as long as the node. Maxillary palp 0.28 (0.24—0.28) times the width of head, third segment 0.85 (0.74—0.88) times as long as second. Fronto-clypeal setae 3 (2—3); setae on mesanepisternum absent, 3 (3—7) setae on mesanepimeron. Wing length 1.9 (1.5—1.9) mm, 2.1 (2.1—2.2) times as long as wide; R5 2.4 (2.1—2.5) times as long as R1; Sc indicated by 5 (5—7) sensory-pores, 4 (4—6) sensory-pores on basal part of R1 and 2 on distal part, 3 pores on medio-distal portion of R5. Tibia of hind leg 0.96 (0.76—0.99) times as long as femur, and second tarsal segment 0.53 (0.47—0.55) times this length; fifth tarsal segment 0.79 (0.74—0.88) times as long as fourth. Distimere (fig. 46) rather inflated, 0.48 (0.48—0.49) times as long as basimere; inferior lamella about half-way narrowly V-shapedly incised

(fig. 47); aedeagus rather slender, a little longer than the rectangular, distally emarginated and often heavily chitinated claspettes.

Female. — Width of head 1.25 (1.23—1.30) times its height. Antenna (figs. 36, 37) with 2 + 12<sup>+</sup> (11—13) segments, its length 1.76 (1.67—1.98) times the width of head; scape ventrally with 2 (2—3) very short, 1 (1—4) lateral and 1 (0—3) dorsal long setae; third flagellomere with its node about as long as (1.00 (1.00—1.08) times) its diameter. Maxillary palp (fig. 104) 0.24 (0.24—0.29) times the width of head; third segment 1.12 (1.00—1.27) times as long as second. Fronto-clypeal setae 2 (0—4); setae on mesanepisternum absent or indistinct, 6 (4—6) setae on mesanepimeron. Wing length 2.1 (1.8—2.1) mm, 2.1 (2.1—2.2) times as long as wide; R5 2.4 (2.3—2.4) times as long as R1; Sc indicated by 4 (4—6) sensory-pores; 4 (4—6) sensory-pores on basal part of R1 and 2 on distal part, 3 pores on medio-distal portion of R5. Tibia of hind leg 0.94 (0.91—0.94) times as long as femur and second tarsal segment 0.51 (0.47—0.52) times this length; fifth tarsal segment about as long as fourth. Tergum 8 triangular (fig. 52), the height of this sclerite about equal to its width. Ovipositor (fig. 59) 1.31 (1.09—1.31) times as long as hind femur, for one-third to about half-way retracted into the eighth abdominal segment; oviduct surrounded by a remarkably chitinated vaginal furca; superior lamella 1.5 (1.5—1.6) times as long as high; inferior lamella very short and truncate (fig. 58).

Immature stages. — Egg length  $\bar{n}$  255  $\mu$ ,  $\bar{n} \pm 2$  SD (95% of egg lengths) between 235—275  $\mu$ ; width  $\bar{n}$  72  $\mu$ . First instar larva (figs. 62, 63); length 255 (212—539), width 97 (85—303)  $\mu$ ; width of head-capsule 29 (26—34), between antennae 12 (11—14)  $\mu$ ,  $n = 17$ ; dorsal spinule-rows 2 (2—0) + 8 (6—8), ventrals 1 (2—0) + 7 (6—7),  $n = 10$ ; respiration apneustic. Second instar (fig. 88); length 632 (506—1248), width 269 (237—679)  $\mu$ ; width of head-capsule 65 (47—71), between antennae 17 (17—22)  $\mu$ ,  $n = 14$ ; dorsal spinule-rows 0 (—1) + 5 (0—8), ventrals 0 (0—2) + 11 (9—11),  $n = 10$ . Third instar (fig. 89—91); length 1596 (948—1691), width 1185 (711—1185)  $\mu$ ; width of head-capsule 73 (59—90), between antennae 19 (19—28)  $\mu$ ,  $n = 31$ ; spathula sternalis large, bilobed (fig. 92, 93), width of spathula 71 (27—71), height 89 (66—102), distance between points of lobes 47 (20—47), height of lobes 27 (19—27), height of median incision 17 (9—17)  $\mu$ ;  $n = 10$ . Pupa length 1627 (1404—1643), prothoracic horns 141 (133—143) and apical papillae 47 (38—53)  $\mu$ ,  $n = 7$ ; sensory-pores situated laterally of the corresponding papillae of the dorsal row (fig. 94).

Papillary pattern (fig. 24a). Dorsal collar papillae absent, one pair of ventral collar papillae. On thoracic segments one pair of dorsal, two pairs of pleural, and one pair of lateral papillae; on Th 1 one pair of sternal papillae, on Th 2 and 3 one pair of ventrals. On segment A 1—7 only one pair of dorsal papillae, one pair of pleural, lateral and ventral papillae; dorsal papillae are absent on A 8, there is one pair of pleural papillae, one pair of laterals and one pair of ventrals; one pair of terminal papillae on AS.

Gall (fig. 99) length 1.7—2.6 mm,  $\bar{n}$  2.1 mm, width 1.7—2.4 mm,  $\bar{n}$  2.0 mm,  $n = 20$ ; galling of the fruit; the fruit is button-like swollen, subrotund, wings are completely or nearly completely reduced; window-pit rather indistinct (*B. pubescens*).

Type material. — Holotype ♂, slide no. 760223.11, The Netherlands, Renkum, 15.i.1975, ex fruit galls of *B. pendula*. Allotype ♀, slide no. 760211.2, The Netherlands, Meyendel, 28.iv.1975, ex fruit galls of *B. pubescens*, leg. J. C. Roskam.

Material (all my localities are from The Netherlands) in coll. Rijksmuseum van Natuurlijke Historie, Leiden. Adults slides no. 760223. 9—10, 760211.1 and 11, males with the same data as the holotype, females as allotype. First instar larva slide no. 750519.3 Duivenvoorde, 19.v.1975, ex female catkins of *B. pubescens*; second instar slide no. 750619.4, Meyendel, 22.vi.1972, ex fruit galls of *B. pubescens*; third instar slide no. 751001.2, same locality as second instar, 1.x.1975; pupa slides no. 730402. 4—6, 9, same locality as second instar, 2.iv.1973, leg. J. C. Roskam. As regards the phenology (see below) this species is the latest, hence the name *tarda*, the retarded. In the sense of Hennig (1966), this is the *Semudobia* species with many apomorphic characters. According to Möhn (1955), three pairs of rows of dorsal papillae seem to be most common in gall midge larvae, and one pair of rows in *S. tarda* therefore must be considered apomorphic. This is the only *Semudobia* species with apneustic first instar larvae. The heavily chitinized genital structures, viz., claspettes in male and vaginal furca in female, only occur in this species. In my opinion, these character stages must also be regarded as apomorphic.

### *Semudobia skuhraevae* sp. nov.

(male: figs. 26, 27, 48, 49; female: figs. 34, 35, 53, 60, 61, 105; imm. stages: figs. 11—13, 66, 69, 82—87, 96, 100)

Male. — Width of head 1.08 (1.08—1.22) times its height. Antenna (figs. 26, 27) with 2 + 13 (12—13) segments, its length 2.32 (2.26—2.49) times the width of head; scape ventrally with one very short, 3 (2—4) lateral and 0 (0—2) dorsal long setae; third flagellomere with its node 1.21 (1.08—1.26) times as long as its diameter; internodes transverse to subquadrate, internode of third flagellomere 0.31 (0.31—0.41) times as long as the node. Maxillary palp 0.28 (0.23—0.31) times the width of head, length of third segment 1.53 (1.05—1.57) times the length of second. Fronto-clypeal setae 4 (1—5); 8 (0—8), often indistinct, setae on mesanepisternum, 8 (4—9) on mesanepimeron. Wing length 2.14 (2.08—2.14) mm, 2.2 (2.2—2.3) times as long as wide; R5 2.2 (2.2—2.4) times as long as R1; Sc indicated by 6 (6—9) sensory-pores, 7 (5—7) pores on basal part of R1 and 2 on distal part, 3 pores on medio-distal portion of R5. Tibia of hind leg 0.84 (0.79—0.87) times as long as femur and second tarsal segment 0.52 (0.47—0.57) times this length; fifth tarsal segment 0.73 (0.73—0.92) times as long as fourth. Distimere (fig. 48) 0.55 (0.52—0.56) times as long as basimere; inferior lamella for about one-third broadly V-shaped incised (fig. 49); aedeagus usually shorter than the verrucose triangular claspettes.

Female. — Width of head 1.19 (1.09—1.19) times its height. Antenna (figs. 34, 35) with 2 + 12 (11+—13) segments, its length 1.61 (1.61—1.87) times the width of head; scape ventrally with 1 (1—2) very short, 3 (3—4) lateral and 4 (2—9) dorsal setae; third flagellomere with its node 1.08 (1.08—1.18) as long as its diameter,

ultimate flagellomere rounded. Maxillary palp (fig. 105) 0.23 (0.23—0.28) times the width of head; length of third segment 1.33 (1.18—1.69) times the length of second. Frontoclypeal setae 5 (1—7); 6 (1—8), often indistinct setae on mesanepisternum, 6 (5—9) setae on mesanepimeron. Wing length 2.14 (2.08—2.14) mm, 2.2 times as long as wide; R5 2.3 times as long as R1; Sc indicated by 4 (4—7) sensory-pores, about 6 pores on basal part and 2 (2—3) on distal part of R1, 3 sensory-pores on medio-distal portion of R5. Tibia of hind leg 0.87 (0.87—0.91) times as long as femur and second tarsal segment 0.54 (0.51—0.55) times this length; fifth tarsal segment 0.79 (0.79—0.85) times as long as fourth. Tergum 8 rectangular to H-shaped (fig. 53). Ovipositor (fig. 61) 0.76 (0.75—0.80) times as long as hind femur, for about one-quarter to half-way retracted into the eighth abdominal segment; vaginal furca not remarkably chitinated; superior lamella 2 times as long as high; inferior lamella rounded, about as long as wide (fig. 60).

Immature stages. — Egg length  $\bar{n}$  359  $\mu$ ,  $\bar{n} \pm 2$  SD (95% of egg lengths) between 335—383  $\mu$ , width  $\bar{n}$  115  $\mu$ . First instar larva (figs. 66—69); length 333 (261—612), width 103 (97—339)  $\mu$ ; width of head-capsule 29 (26—37), between antennae 17 (12—17)  $\mu$ ; dorsal spinule-rows 4 (3—4) + 8 (7—8), ventrals 4 (3—4) + 7 (7—8),  $n = 10$ ; respiration metapneustic. Second instar (fig. 82); length 679 (442—1059), width 332 (221—727)  $\mu$ ; width of head-capsule 67 (48—79), between antennae 21 (16—26)  $\mu$ ,  $n = 39$ ; dorsal spinule-rows absent, ventrals 0 (2—0) + 6 (6—8),  $n = 10$ . Third instar (fig. 83—85); length 1675 (1138—2022), width 932 (758—1329)  $\mu$ ; width of head-capsule 85 (67—112), between antennae 23 (23—34)  $\mu$ ,  $n = 41$ ; spathula sternalis extremely variable (figs. 86, 87), more or less bilobed with a variable number (0—6) of small teeth between the usually larger, pointed, lobes, width of spathula 17 (17—44), height 14 (14—20), distance between points of lobes 11 (11—35), height of lobes 3 (3—9), height of smaller, median teeth 2 (2—3)  $\mu$ ,  $n = 10$ . Pupa length 1547 (1117—1786), prothoracic horns 114 (114—160) and apical papillae 42 (38—60)  $\mu$ ,  $n = 10$ ; sensory-pores between the corresponding papillae of the second and third pairs of dorsal rows (fig. 96).

Papillary pattern (fig. 24e). One pair of dorsal collar papillae and two pairs of ventral collar papillae on SS (only visible in first instar). On thoracic segments two pairs of dorsal papillae, two pairs of pleurals, two pairs of laterals; on Th 1 one pair of sternal papillae and on Th 2 and 3 one pair of ventrals. On segments A 1—7 three pairs of dorsal papillae, one pair of pleurals, one pair of laterals, two pairs of ventral papillae; on A 8 one pair of dorsal, one pair of pleural, one pair of lateral, and one pair of ventral papillae; 2—3 pairs of terminal papillae on AS.

Gall (fig. 100) length 1.4—2.0 mm,  $\bar{n}$  1.8 mm, width 1.0—1.2 mm,  $\bar{n}$  1.1 mm,  $n = 20$ ; galling of the "bract"; the ovoid gall is situated between the spindle of the catkin and the scale; window-pit absent (*B. pubescens*). In Japanese (Honshu, Azegate, *B. ermanii*) and American (South Dakota, Black Hills, *B. occidentalis*) material *S. skuhravae* is found in fruit galls. These galls have no window-pit and are coalescent with the scale. When gall and scale are separated, the membranous cocoon of the larva becomes visible.

Type material. — Holotype ♂, slide no. 760223.4, Allotype ♀, slide no. 760209.1, The Netherlands, Renkum, 15.i.1975, ex bract galls of *B. pendula*, leg. J. C. Roskam.

Material (all my localities are from The Netherlands) in coll. Rijksmuseum van Natuurlijke Historie, Leiden. Adults slides no. 760223.3, 5—6, 750115.2—3, 760209.2, 760216.2, same data as type material. First instar larva slide no. 750519.6, Duivenvoorde, 19.v.1975, ex catkins of *B. pubescens*; second instar slide no. 750619.7, same locality as first instar, 19.vi.1975, ex bract galls of *B. pubescens*; third instar slide no. 720713.2, Meyendel, 13.vii.1972, ex bract galls of *B. pubescens*. Pupa slide no. 730328.2—3, same locality as third instar, 28.iii.1973, leg. J. C. Roskam.

This species is named after dr. Marcelá Skuhrová, Prague, Czechoslovakia. She was first (Skuhravá & Skuhrový, 1960, 1963) in suggesting the species to be different from *Semudobia betulae*, remarking the correlation of this midge with the bract gall. Moreover she was the first to depict the spathula. In this species all three pairs of rows of dorsal papillae are developed on A 1—7, and so it is most similar to the usual state of papillary pattern in Cecidomyiidae (Möhn, 1955). Because all other *Semudobia* species have less than three pairs of rows, three pairs of rows of dorsal papillae must be considered a plesiomorphic character. On the ventral surface of larvae of *S. skuhrovae* the papillary pattern is also very complete: always two pairs of rows of lateral papillae on thoracic segments and two pairs of rows of ventrals on the abdomen. In my opinion these characters of lateral and ventral papillae must be considered a primitive condition in the genus. If we combine the plesiomorphic characters with character states of other semaphoronts, we must conclude that relatively big eggs (this results in a relatively small number of egg per female: about 50 in *S. skuhrovae*, about 120 in *S. tarda*) may also indicate a primitive condition. In this way, the galling of the bract may be a primitive condition, too. In adults the situation is more problematic. Gagné (1976) stated that a relatively large number of flagellomeres should be an apomorphic character. In *Semudobia* relatively large numbers of flagellomeres occur in *S. skuhrovae*, with plesiomorphic characters in the larval papillary pattern, and in *S. steenisi*, which shares apomorphic characters with *S. betulae* and *S. brevipalpis* in the larval stages.

#### DISTRIBUTION

*Semudobia* midges depend entirely on *Betula* species. Therefore, their geographical distribution must be expected to be wholly or partially the same as that of *Betula*. *Betula* occurs in the whole boreal and temperate part of the Holarctic region (Meusel et al., 1965). For such a huge area, even after years of sampling, the picture can only be very incomplete. Therefore, many more data are needed to get a true understanding of the distribution of *Semudobia* species. Much material for the present study was collected in western Europe. A collecting trip to the U.S.A. resulted in many data on the distribution of *Semudobia*, especially in the Black Hills and the Rocky Mountains. During a year, a graduate student had the opportunity to study insects of birch catkins in Japan. Several samples of birch catkins were collected by colleagues in Canada and Eastern Russia. Finally, many of the present data are based on infections found in plant specimens from the collections of the Rijksherbarium, Leiden and the Herbarium Vadense, Wagningen.



			<i>S. skuhravae</i>	<i>S. tarda</i>	<i>S. betulae</i>	<i>S. brevipalpis</i>	<i>S. steenisi</i>
America	East-Canada	Montreal	-	-	-	+	-
		Ontario	-	-	+	+	-
		Quebec	-	+	-	+	-
	West-Canada	Alberta	+	-	-	-	-
		Br. Columbia	-	-	-	-	+
	East-U.S.A.	Connecticut	+	-	-	+	-
		Pennsylvania	-	-	+	+	-
		Washington DC	-	-	-	+	-
	West-U.S.A.	Colorado	+	-	-	-	+
		Montana	+	+	-	-	+
South Dakota		+	-	-	-	-	
Wyoming		+	-	-	-	+	
Europe	Austria	+	+	+	-	-	
	Belgium	+	+	+	-	-	
	Czechoslovakia	+	+	+	-	-	
	Denmark	+	+	+	-	-	
	France	+	+	+	-	-	
	Germany	+	+	+	-	-	
	Great Britain	+	+	+	-	-	
	Ireland	+	+	+	-	-	
	The Netherlands	+	+	+	-	-	
	Norway	+	+	+	-	-	
	Poland	+	+	+	-	-	
	Soviet-Union Latvia	+	+	+	-	-	
	Sweden	+	+	+	-	-	
	Switzerland	+	+	+	-	-	
Asia	Japan	+	+	+	-	-	
	Soviet-Union Baikal Lake	+	-	-	-	-	
	Kamtschatica	-	-	+	-	-	
	Kirgistania	+	+	+	-	-	
	Nerchinsk	+	-	-	-	-	
	Wladiwostok	+	+	+	-	-	

Table 1. Geographical distribution of *Semudobia*.

Table 1 shows a mainly Palaearctic distribution for *S. betulae* and *S. tarda*. When I collected these gall midges in the U.S.A., this was always on introduced European *B. pendula*. Also in Canada, where *S. betulae* and *S. tarda* were collected on *B. populifolia* and *B. papyrifera*, respectively, an introduction of infected fruits of Palaearctic birch species is supposed.

In North America two species of the "*S. betulae* complex" are present: *S. brevipalpis* in the eastern states of Canada and the U.S.A.; *S. steenisi* in the western states including Rocky Mountains. A similar vicariance occurs in the host plant. European *Betula pubescens* is replaced in eastern North America by *B. papyrifera* and in western North America by *B. occidentalis*. The vicariance in

Station	number of galls		% infected fruits	<i>S. betulae</i>	<i>S. tarda</i>	<i>S. skuhravae</i>	$\frac{S. betulae}{S. tarda}$
a							
Kootwijk	1	199	1.22	155	10	34	15.50
	2	715	1.30	614	101	-	6.08
	3	495	2.75	418	40	37	10.45
	4	2945	5.26	2397	248	300	9.67
	5	369	5.58	253	112	4	2.26
	6	126	0.72	110	3	13	36.67
Meyendel	1	486	5.31	293	125	68	2.34
	2	545	5.50	226	159	160	1.49
	3	2323	15.43	2100	204	19	10.29
Duivenvoorde		2045	9.11	905	551	589	1.64
Binnen-Buiten							
Liede		1174	6.15	753	337	84	2.23
Nieuwkoop		5742	11.82	3099	2259	384	1.37
Ilperveld	1	1011	5.10	468	537	6	0.87
	2	842	2.66	454	386	2	1.18
b							
Kootwijk	1	138	0.37	110	24	4	4.58
	2	558	1.24	370	80	108	4.63
	3	161	0.28	124	12	25	10.33
	4	367	0.71	264	98	5	2.69
	5	1210	2.54	1035	164	11	6.31
	6	190	0.70	172	6	12	28.67
Meyendel	1	1374	5.72	833	443	98	1.88
	2	1042	3.53	795	223	24	3.57
	3	5752	10.87	3777	1709	266	2.21
Duivenvoorde		3274	4.70	873	2310	91	0.38
Binnen-Buiten							
Liede		949	2.43	386	518	45	0.75
Nieuwkoop		5312	6.13	2329	2853	130	0.82
Ilperveld	1	3817	6.43	1770	2041	6	0.87
	2	875	1.98	325	533	17	0.61

Table 2. Occurrence of *Semudobia* species in different study areas during the year 1976. a, early spring; b, late summer.

eastern Asia of *B. pubescens* by *B. davurica* seems not to have been followed by a vicariance in *Semudobia*: all Japanese and East-Russian specimens of *S. betulae* (as are those of *S. tarda* and *S. skuhravae*) are very similar to the European material.

It is of interest to note that *S. betulae* and *S. tarda* both are gall inducers in birch fruits; they usually may be found together in the same birch populations. If different habitats are sampled, the two species seem to be ecologically different. In 1976, the frequency of occurrence of *Semudobia* species in fourteen birch populations of six areas was determined (Table 2). In each population about eight trees were marked; in each sampling series a constant number of catkins were collected. Two series were made, where possible from the same trees, one in early spring just before the emergence of the midges and one in late summer, when infections caused by this generation of midges could be easily recognised.

The study areas. — Kootwijk (52.11 N 5.46 E) is a very dry sandy area where *B. pendula* is abundant. Meyendel (52.08 N 4.20 E) is a dune area with a rather heterogeneous structure: *B. pendula* can usually be found on relatively dry sand dunes, whereas *B. pubescens* is common in the wetter valleys. Duivenvoorde (52.06 N 4.24 E) is a rather wet area, overgrown with blackberry brakes and rushes; of the two birch species, *B. pubescens* dominates here. Binnen-Buiten Liede (52.23 N 4.41 E), Nieuwkoop (52.10 N 4.50 E), and Ilperveld (52.29 N 4.58 E) are very wet bogs; here again, *B. pubescens* is the dominant birch species. In the dry habitat Kootwijk populations, 78% or more of the fruit infections is caused by *S. betulae* (except Kootwijk 5, a young population). In wetter habitats (Duivenvoorde, Liede, Nieuwkoop and Ilperveld), the *S. tarda* part of the fruit infections, especially in the "b" series, is relatively large (44% or more). In the "scattered" Meyendel area both infection "types" are represented with *S. betulae* predominant; there is no distinct correlation with a wet or a dry habitat.

In Switzerland five birch populations at different altitudes were studied. In the areas Kerenzerberg (47.07 N 9.08 E, alt. 600 m), Walenstadtberg (47.08 N 9.18 E, alt. 800 m) and Boggenberg (47.06 N 9.01 E, alt. 1250 m) *S. betulae*, *S. tarda* and *S. skuhravae* were all common; in the area Ahornen (47.05 N 9.00 E, alt. 1400 m), *S. tarda* was absent and at Stausee Garichte (46.57 N 9.06 E, alt. 1600 m), *S. betulae* was the only gall-inducing midge.

Latitude offers a similar pattern. In Norway, galls were collected in nine areas, varying in North latitude from 58.33 to 64.30. In the two most northern localities, Tunnsjö (64.45 N 13.00 E, alt. 750 m) and Kongsvoll (63.33 N 9.24 E, alt. 1000 m), only *S. betulae* was present. In most other localities, both *S. skuhravae* and *S. betulae* were common. The localities of this series where *S. tarda* was also present are Åseral (58.33 N 7.24 E, alt. 250 m) and Ossjoën (61.20 N 11.30 E, alt. 500 m).

The reason why *S. tarda* is absent at high altitudes and/or latitudes may be a phenological one. *S. tarda* is the latest in pupation (pag. 181); for this species the vegetation period in these extreme areas may be too short to complete larval development.

The southern-most locality in western Europe, where *Semudobia* infections were found, is Saintes in France (45.45 N 0.45 W); *S. betulae* and *S. tarda* both are abundant there. In Japan the most southern locality is Honshu, Azegate (36.44 N 139.27 E, alt. 1280 m); there *S. skuhravae* is the only gall inducer.

In Europe, *S. betulae*, *S. tarda* and *S. skuhravae* regularly occur together; this seems to be different in the Nearctic Region. In Canada and the U.S.A. 20 infected birch populations were sampled (populations with introduced Palaearctic species excluded). In only 6 populations *S. skuhravae* was found together with either *S. brevipalpis* or *S. steenisi*; in 7 populations *S. skuhravae* was the only gall inducer, in 4 populations this was *S. brevipalpis* and in 3 populations *S. steenisi*. It is of some interest to mention that in one large area (Black Hills, South Dakota) four birch populations (*B. occidentalis* and *B. papyrifera*) could be detected with *Semudobia* infections. In all these cases *S. skuhravae* was the only gall inducer.

#### LIST OF HOST PLANTS

Besides the fresh material, about 300 herbarium specimens with fruit catkins were investigated on *Semudobia* infections. Kuzneva (in Komarov, 1936), Rehder (1940), and Ohwi (1965) were used for the identification of birch taxa. The nomenclature is according to Kruessmann (1960) and Fontaine (1970). The taxa are listed in Table 3. Absence of infections by certain gall midge species of taxa marked by an asterisk may be due to the small sample size.

The genus *Betula* may be divided into four sections. The section *Acuminatae* is exclusively East Asiatic. The section *Costatae* has a disjunct areal: some of the species are East Asiatic, other species are only found in the eastern part of North America. The section *Excelsae* is Holarctic and the section *Humiles* is mainly Circumpolar. None of the species belonging to the section *Acuminatae* were infected at all. In the section *Costatae* infections are mainly common in the East Asiatic species: *B. costata*, *ermanii*, *grossa*, *jacquemontii* and *raddeana*; here, *S. skuhravae* is the most common gall inducer. In East American *B. alleghaniensis* infections occur, but they are very rare (*S. skuhravae*, one gall in one cultivated specimen only). The absence of infections in *B. lenta* may be explained by the very typical odour of the cherry birch, which may act as a repellent compound for *Semudobia*. Also in the section *Humiles*, *S. skuhravae* seems to be the predominant species. *B. nana* deserves special attention. Bachmaier (1965) reported that infections of *Semudobia* are not rare. In more than 30 specimens, however, I found only one single gall of *Semudobia* in a Norwegian sample. In Einsiedeln, Switzerland (47.07 N 8.45 E, alt. 900 m), a heather with *B. nana* is mixed with and surrounded by normally infested *B. pubescens*; although flowering times of *B. nana* and *B. pubescens* coincide (Hegi, 1957), no infections of *Semudobia* were found in those dwarf birches. In Åseral, Norway (58.33 N 7.24 E), a bog with *B. nana* mixed with *B. pubescens* and their hybrid *B. × intermedia* was visited. Both *B. pubescens* and *B. × intermedia* were crammed with *Semudobia* infections. Here, again, not a single gall was found in *B. nana*. Finally, infections are common in most species of the section *Excelsae*.

#### PHENOLOGY

In The Netherlands (Meyendel), the respective ontogenetic stages were observed in the following periods of 1976 (Table 4). In fig. 25, some differences in

Section	Species	<i>S. skuhravae</i>	<i>S. tarda</i>	<i>S. betulae</i>	<i>S. brevipalpis</i>	<i>S. steeniei</i>
Acuminatae (Regel).	★ <i>B. alnoides</i> Buch.-Ham.	-	-	-	-	-
	★ <i>B. cylindrostachya</i> Lindl. apud Wallich	-	-	-	-	-
	<i>B. marimowicziana</i> Regel	-	-	-	-	-
Costatae (Regel).	★ <i>B. albo-sinensis</i> Burkill	-	-	-	-	-
	<i>B. alleghantensis</i> Brit.	c	-	-	-	-
	★ <i>B. corylifolia</i> Regel & Maxim.	c	-	-	-	-
	<i>B. costata</i> Trautv.	+	+	-	-	-
	<i>B. ermanii</i> Cham.	+	c	c	-	-
	<i>B. forrestii</i> (W.W.Sm.) Hand.-Mazz.	-	-	-	-	-
	<i>B. grossa</i> Sieb. & Zucc.	+	c	-	-	-
	<i>B. jacquemontii</i> Spach.	c	-	c	-	-
	<i>B. lenta</i> L.	-	-	-	-	-
	★ <i>B. medwediewii</i> Regel	-	+	-	-	-
	★ <i>B. nigra</i> L.	-	-	-	-	-
	★ <i>B. raddeana</i> Trautv.	c	-	c	-	-
	★ <i>B. schmidtii</i> Regel	-	-	-	-	-
	<i>B. utilis</i> D. Don	+	+	-	-	-
Excelsae (Koch).	★ <i>B. chichibuensis</i> Hara	-	-	-	-	-
	★ <i>B. x coerulea</i> Blanchard	c	c	-	-	-
	★ <i>B. coerulea-grandis</i> Blanchard	c	-	-	-	-
	★ <i>B. celtiberica</i> Rothm. & Vasc.	-	-	-	-	-
	<i>B. davurica</i> Pall.	-	-	-	-	-
	<i>B. x intermedia</i> (Hartm.) Thomas	+	-	+	-	-
	★ <i>B. kirghisorum</i> Sav.	+	+	+	-	-
	★ <i>B. litwinowii</i> Doluch.	c	-	c	-	-
	<i>B. occidentalis</i> Hook.	+	-	-	-	+
	<i>B. papyrifera</i> Marsh.	+	c	c	+	-
	<i>B. pendula</i> Roth	+	+	+	-	-
	<i>B. platyphylla</i> Suk.	+	+	+	-	-
	<i>B. populifolia</i> Marsh.	c	-	c	+	-
	<i>B. pubescens</i> Ehrh.	+	+	+	-	-
	ssp. <i>carpathica</i> , ssp. <i>murithii</i>	+	+	+	-	-
	★ <i>B. turkestanica</i> Litv.	+	-	-	-	-
Humiles (Koch).	★ <i>B. apoensis</i> Nakai	-	-	-	-	-
	★ <i>B. x borggraveana</i> Zabel	c	-	c	-	-
	★ <i>B. fruticosa</i> Pall.	+	-	-	-	-
	★ <i>B. glandulifera</i> (Regel) Butler	-	-	-	-	-
	<i>B. glandulosa</i> Michx.	+	-	-	-	-
	★ <i>B. humilis</i> Schrank	c	+	+	-	-
	★ <i>B. middendorffii</i> Trautv.	-	-	c	-	-
	<i>B. nana</i> L.	(+)	-	-	-	-
	<i>B. pumila</i> L.	+	-	-	-	-
	★ <i>B. x purpusii</i> Schneid.	-	-	-	-	-
	★ <i>B. tatewakiana</i> M. Ohki & S. Watanabe	-	-	-	-	-

Table 3. List of host plants. + infections under natural conditions; c, infections in plants, cultivated outside their distribution area, e.g. botanical gardens; (\*) less than 5 specimens studied.

phenology of the Palaearctic species are demonstrated. *S. skuhravae* is the earliest species to pupate, *S. tarda* the latest; *S. betulae* is the first in passing the first and second stages.

Effects of different altitudes on phenology were studied in Switzerland. In Walenstadtberg (alt. 800 m), situated on a sunny slope above the Walensee, no remarkable differences with The Netherlands (Meyendel), were found. On

Table 4. Phenology of Palaearctic *Semudobia* species.

stage	period
third instar larva	until 12.iv
pupa	15.iii — 1.v
adult	20.iv — 9.v
egg	28.iv — 15.v
first instar larva	8.v — 23.vi
second instar larva	9.vi — 12.vii
third instar larva	from 16.vi

Boggenberg (alt. 1250 m), *Semudobia* appears about three weeks later, but in Ahornen (alt. 1400 m) and at Stausee Garichte (alt. 1600 m) no eggs were observed before the end of May, and at the end of July only first and second instar larvae were found. Third instar larvae were collected in the last week of August at Ahornen and Stausee Garichte.

Similar effects on the phenology are observed at high latitude. In the first half of July, 1976, infections of *Semudobia* were observed in eight areas in Norway (61.20 N — 64.30 N). Most localities are situated at about 950 m alt. In six areas only first instar larvae were present at that date; in only two cases, Ossjoën (61.20 N 11.30 E, alt. 500 m) and Rindal (63.05 N 8.30 E, sea level), also second instar larvae could be collected.

The full-grown larva of *Semudobia* undergoes diapausis; it is impossible to rear adults unless they have passed a cold period. In one case (Wyoming, Wind River), larvae of *S. steenisi*, collected in September, 1976, and, transferred to my room, pupated and gave rise to adults in the beginning of October. A similar absence of diapausal condition must have occurred in the material of Forsius (1927), who got adults in August.

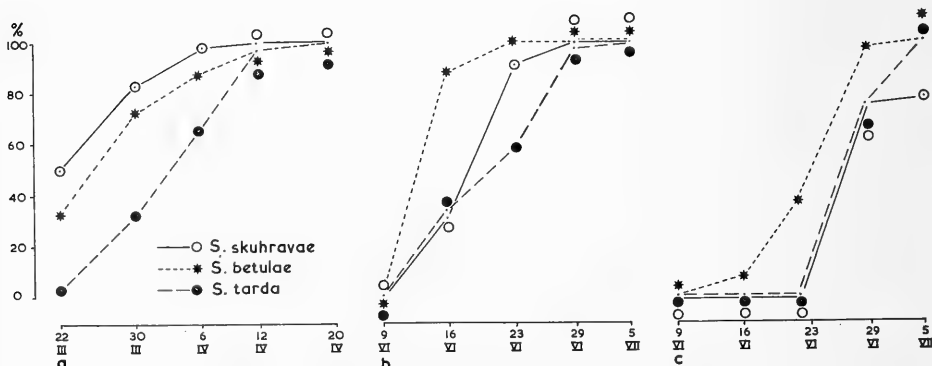


Fig. 25. Phenology of *Semudobia*. a, % pupated midges; b, % animals that passed first stage moulting; c, % animals that passed second stage moulting.

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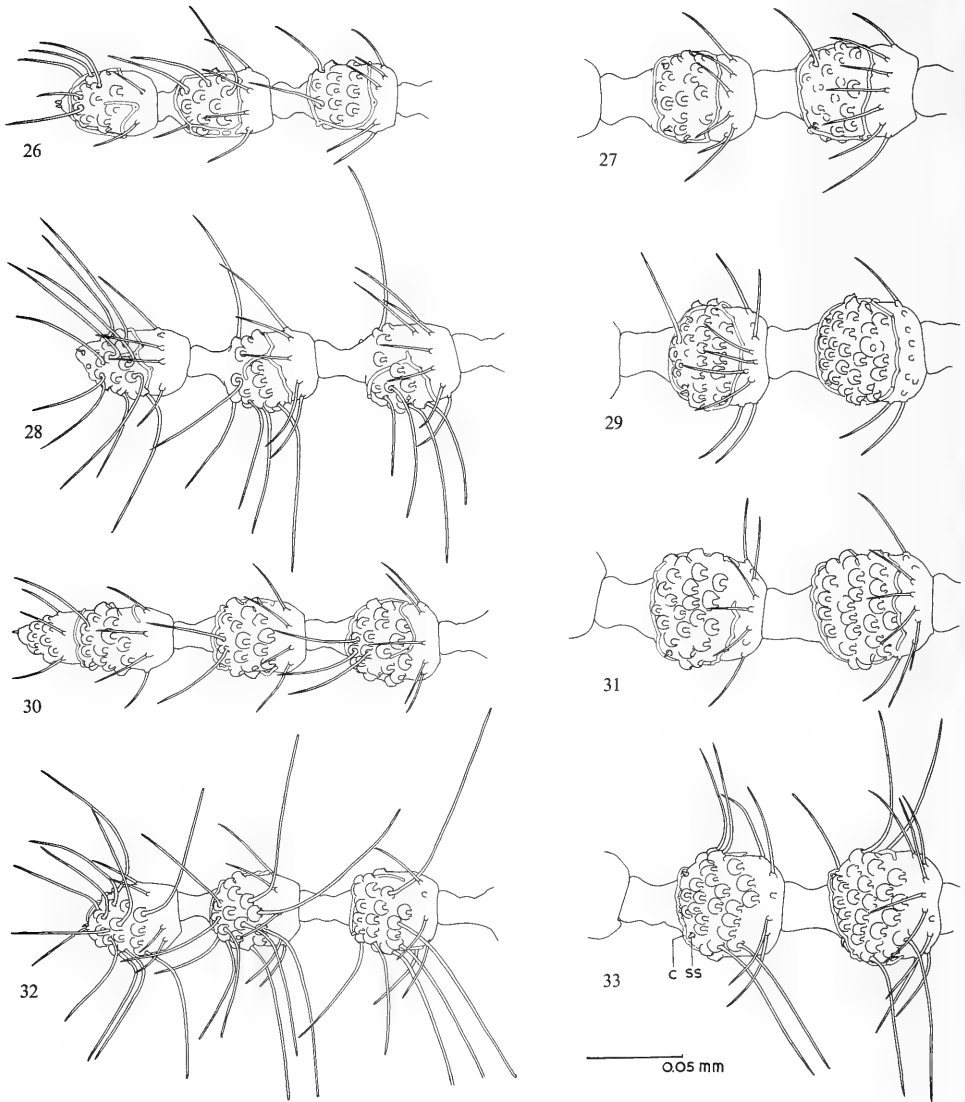
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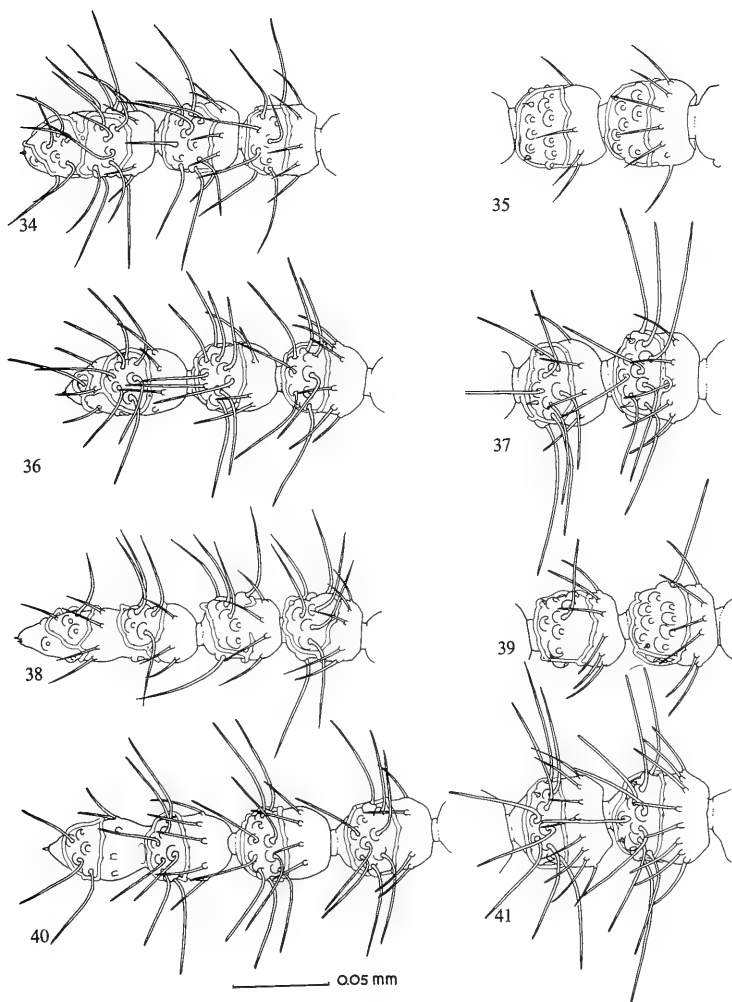
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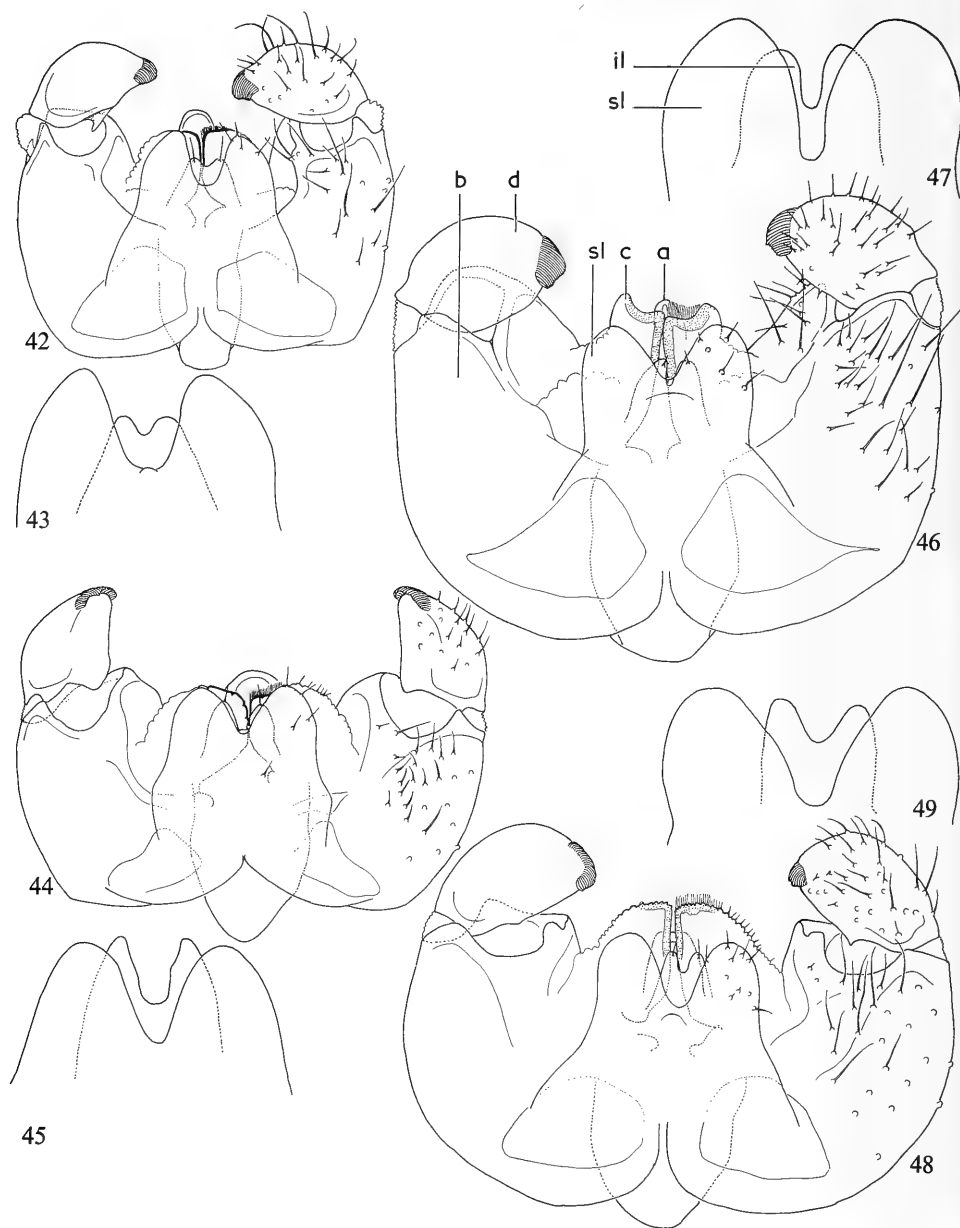
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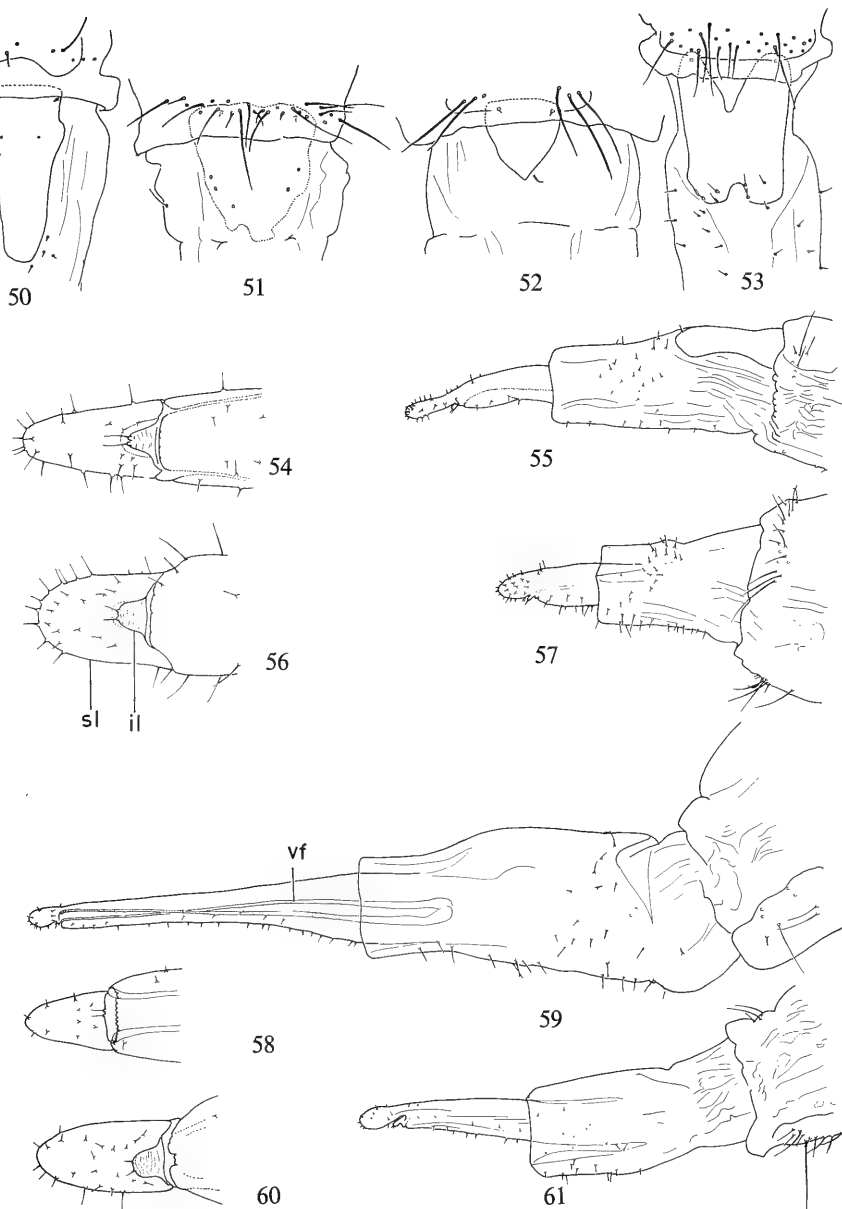
Figs. 26—33. Fifth, sixth and ultimate antennal segments, ♂. 26—27, *S. skuhravae*; 28—29, *S. tarda*; 30—31, *S. brevipalpis*; 32—33, *S. betulae*. c, circumfila; ss, sensorial spine.



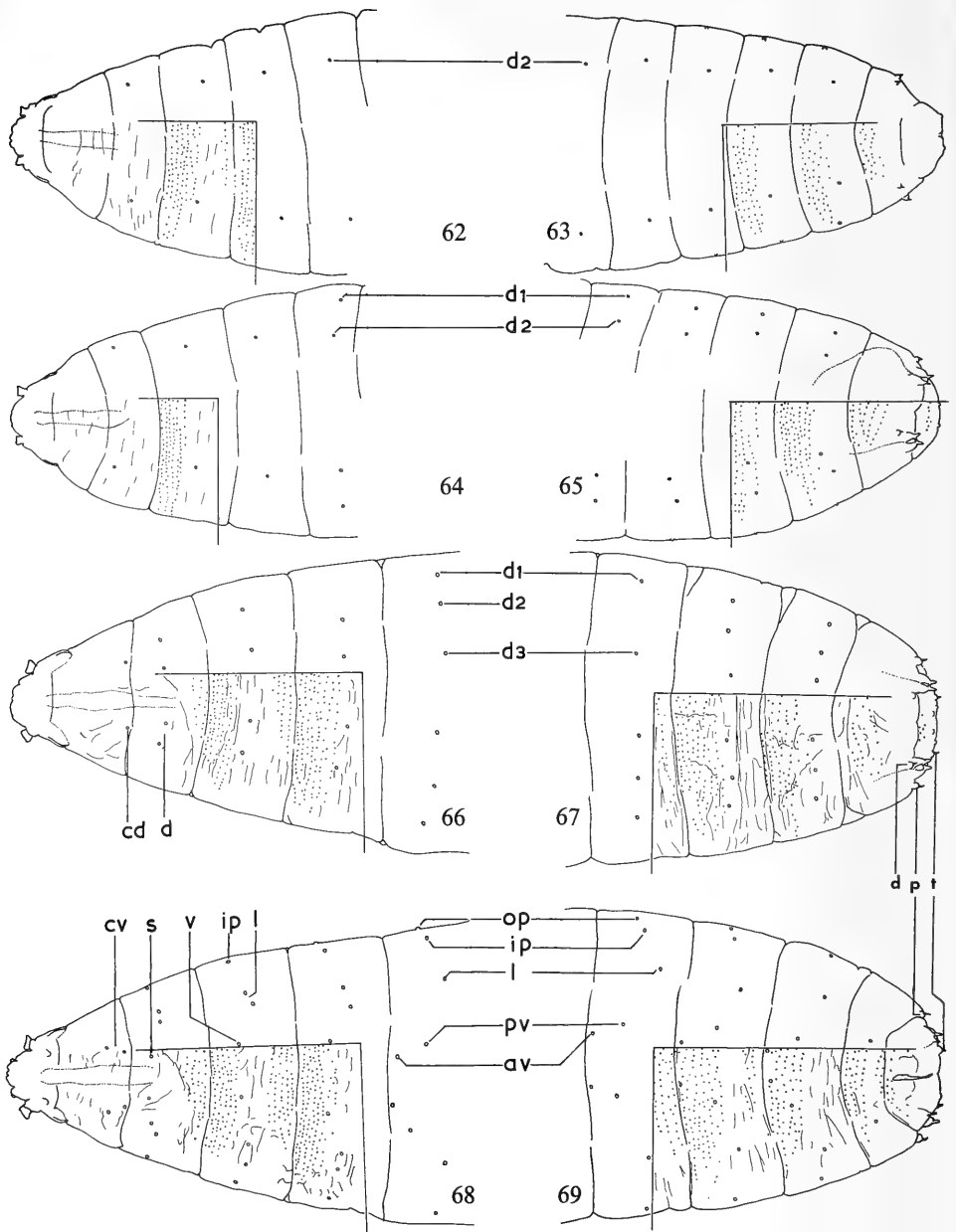
Figs. 34—41. Fifth, sixth and ultimate antennal segments, ♀. 34—35, *S. skuhravae*; 36—37, *S. tarda*; 38—39, *S. brevipalpis*; 40—41, *S. betulae*.



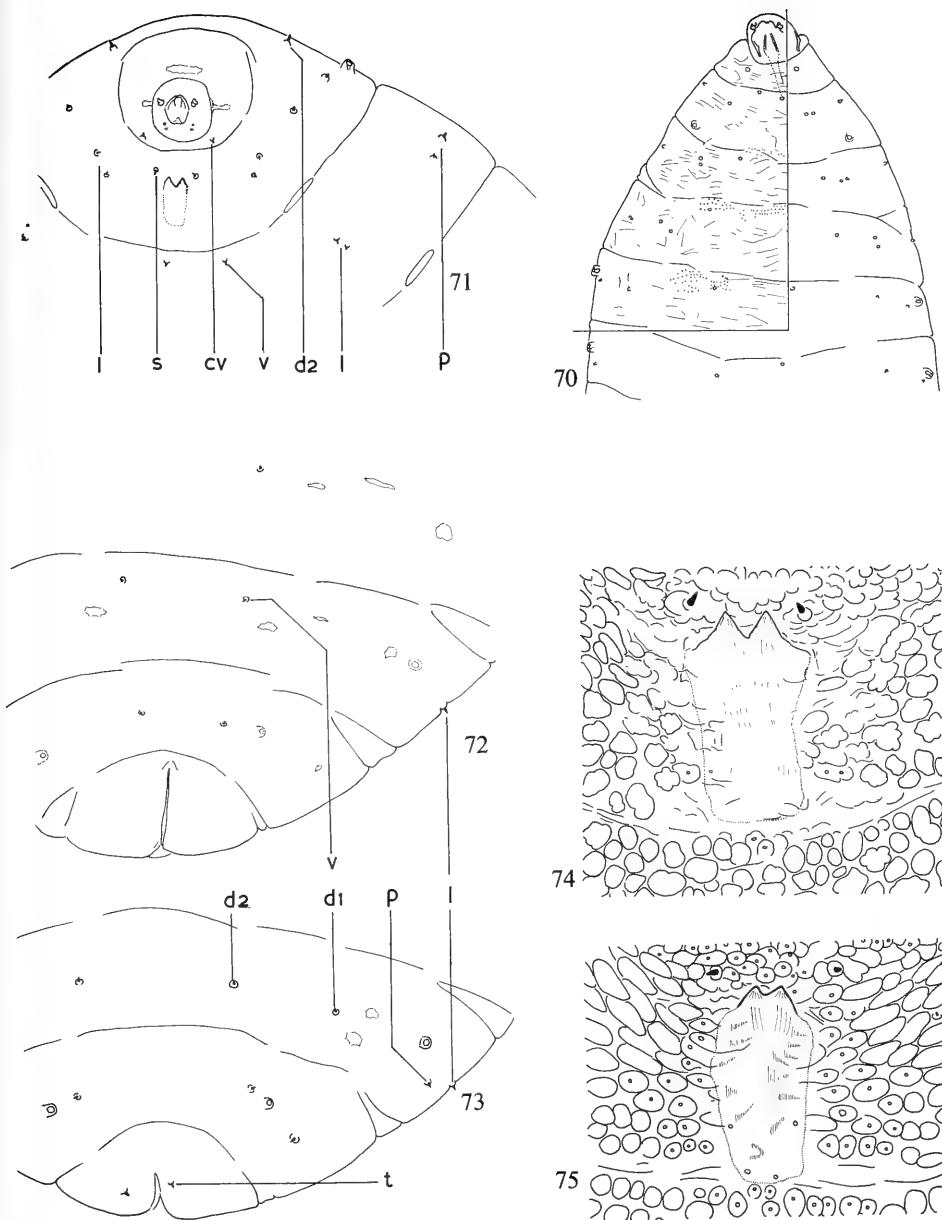
Figs. 42, 44, 46, 48, male genitalia, dorsal aspect; 43, 45, 47, 49, detail of superior and inferior lamella: 42—43, *S. betulae*, 44—45, *S. brevipalpis*, 46—47, *S. tarda*, 48—49, *S. skuhravae*. a, aedeagus; b, basimere; c, claspette; d, distimere; il, inferior lamella; sl, superior lamella. 42, 44, 46, 48,  $\times 220$ ; 43, 45, 47, 49,  $\times 400$ .



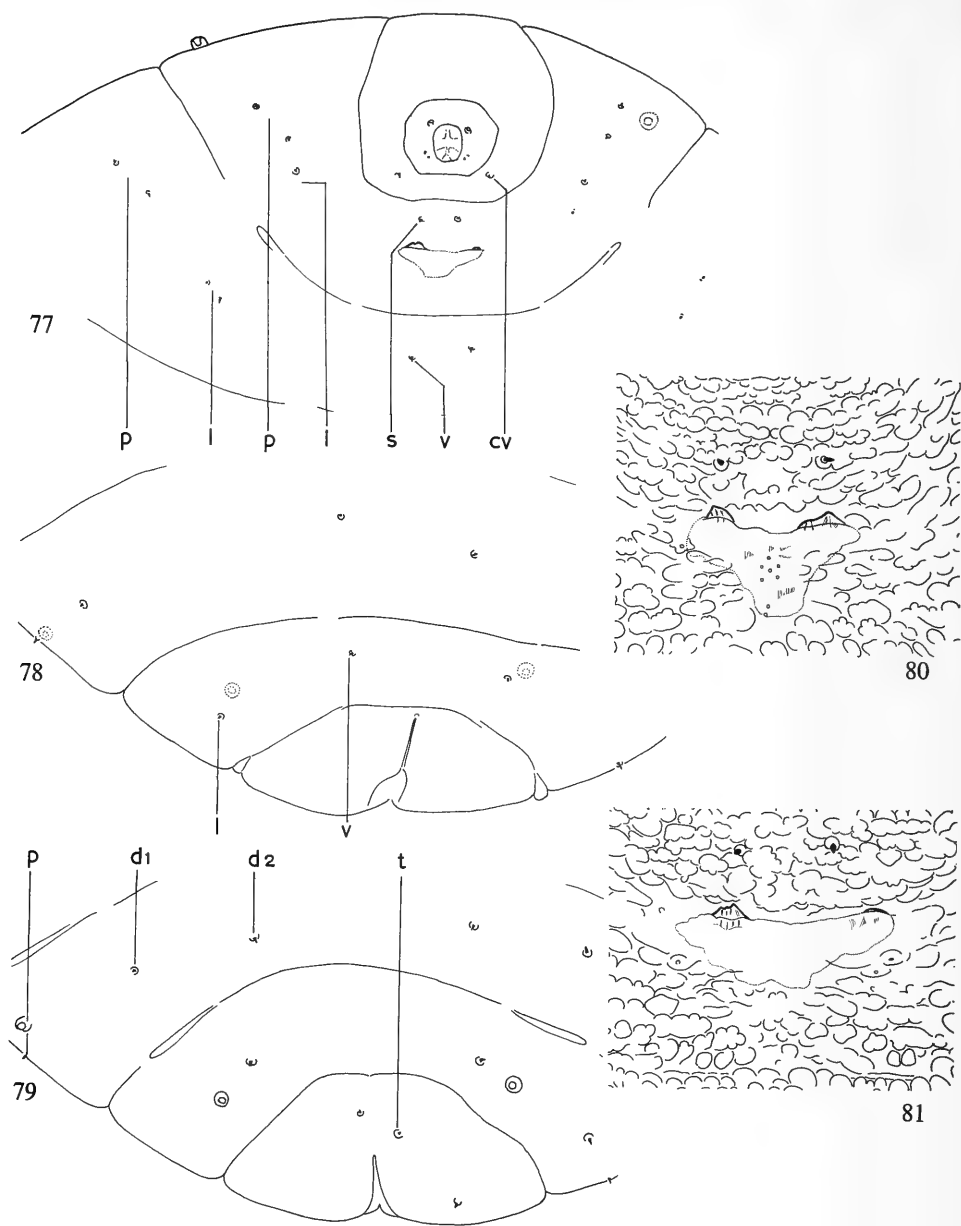
Figs. 50—53, female eighth tergum; 54, 56, 58, 60, detail of female superior and inferior lamella, ventral aspect; 55, 57, 59, 61, ovipositor, lateral aspect: 50, 54, 55, *S. betulae*; 51, 56, 57, *S. brevipalpis*; 52, 58, 59, *S. tarda*; 53, 60, 61, *S. skuhravae*. il, inferior lamella; sl, superior lamella; vf, vaginal furca. 50—53,  $\times 120$ ; 54, 56, 58, 60,  $\times 260$ ; 55, 57, 59, 61,  $\times 85$ .



Figs. 62—69. First instar larva. 62, 64, 66, head and thorax, dorsal aspect; 68, ditto, ventral aspect; 63, 65, 67, sixth to eighth abdominal segment and anal segment, dorsal aspect; 69, ditto, ventral aspect: 62—63 *S. tarda*; 64—65 *S. betulae*; 66—69 *S. skuhravae*; av, anterior ventral papilla; cd, dorsal collar papilla; cv, ventral collar papilla; d, d1—3, dorsal papilla; ip, inner pleural papilla; l, lateral papilla; op, outer pleural papilla; p, pleural papilla; pv, posterior ventral papilla; s, sternal papilla; t, terminal papilla; v, ventral papilla.  $\times 400$ .

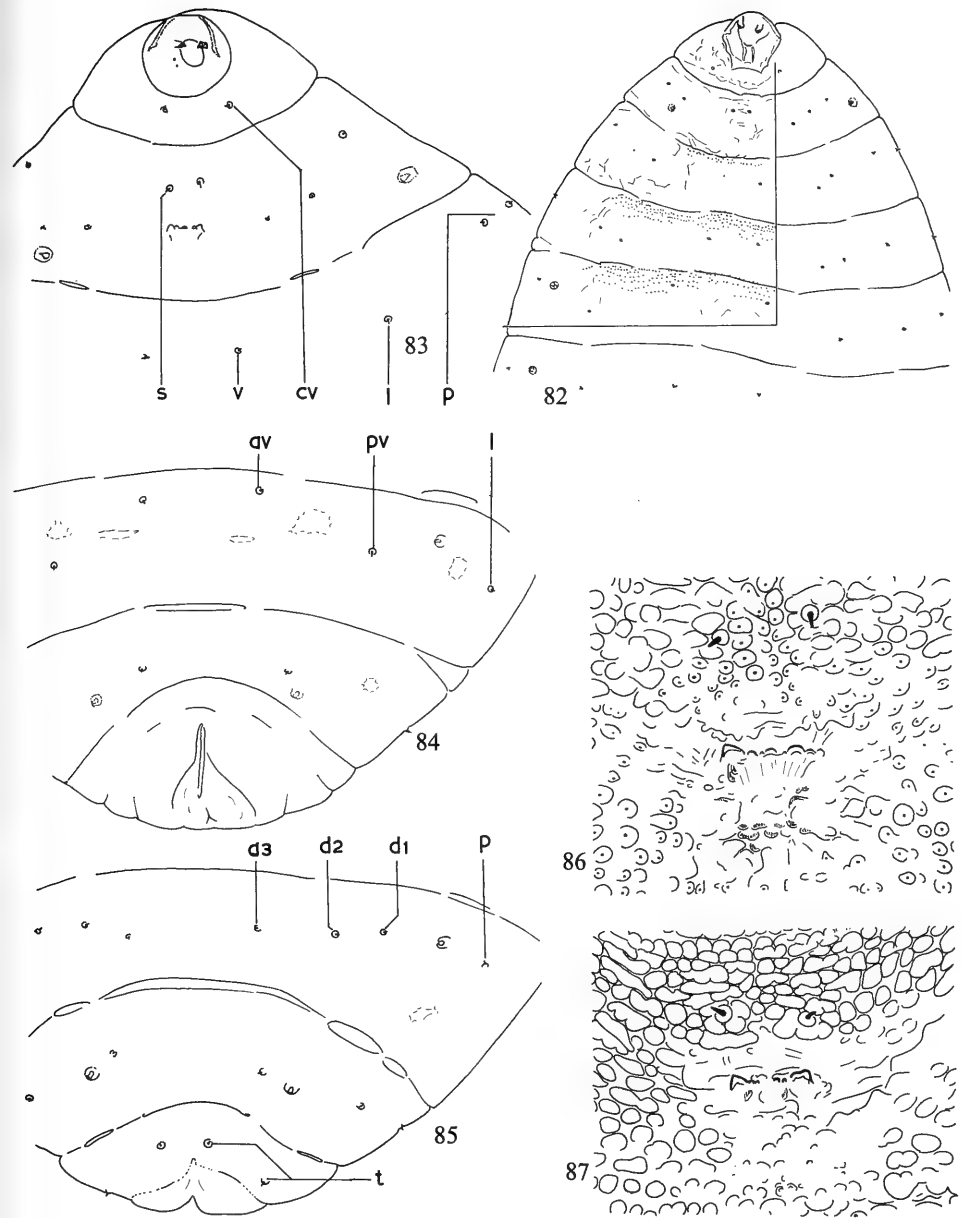


Figs. 70—75. *S. betulae*. 70, head and thorax of second instar, ventral aspect; 71, head, supernumerary segment and first thoracic segment of third instar, ventral aspect; 72, seventh and eighth abdominal segments and anal segment of third instar, ventral aspect; 73, ditto, dorsal aspect; 74—75, spathula sternalis: 74, The Netherlands, Meyndel, 75, Kamtschatka. For explanation of symbols, see figs. 62—69. 70—73,  $\times 140$ ; 74—75,  $\times 425$ .

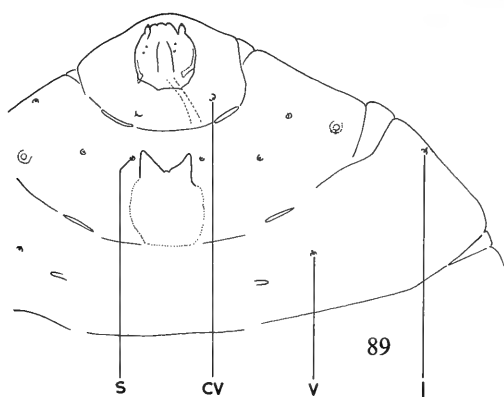


Figs. 77—81. *S. brevipalpis*. 77, head, supernumerary segment and first thoracic segment of third instar, ventral aspect; 78, seventh and eighth abdominal segments and anal segment of third instar, ventral aspect; 79, ditto, dorsal aspect; 80—81, spathula sternalis: 80, U.S.A., Washington DC., 81, Canada, Quebec. For explanation of symbols, see figs. 62—69. 77—79,  $\times 140$ ; 80—81,  $\times 425$ .



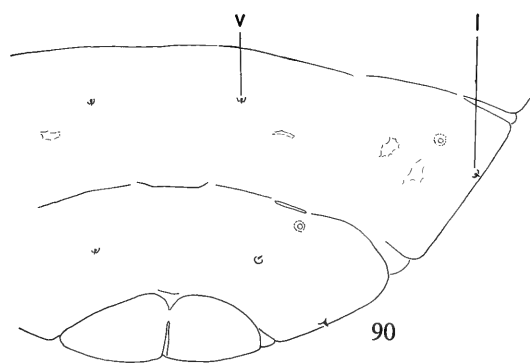
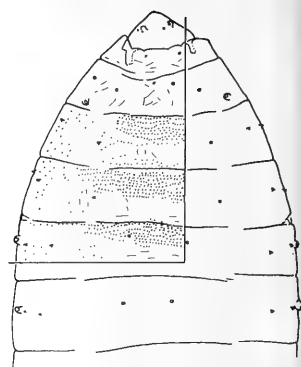


Figs. 82—87. *S. skuhraevae*. 82, head and thorax of second instar, ventral aspect; 83, head, supernumerary segment and first thoracic segment of third instar, ventral aspect; 84, seventh and eighth abdominal segments and anal segment of third instar, ventral aspect; 85, ditto, dorsal aspect; 86—87, spatula sternalis: 86, The Netherlands, Meyendel, 87, Canada, Alberta. For explanation of symbols, see figs. 62—69. 82—85,  $\times 140$ ; 86—87,  $\times 425$ .



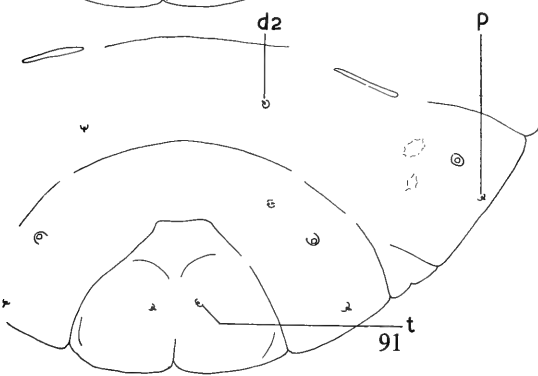
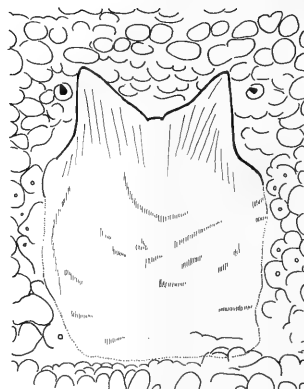
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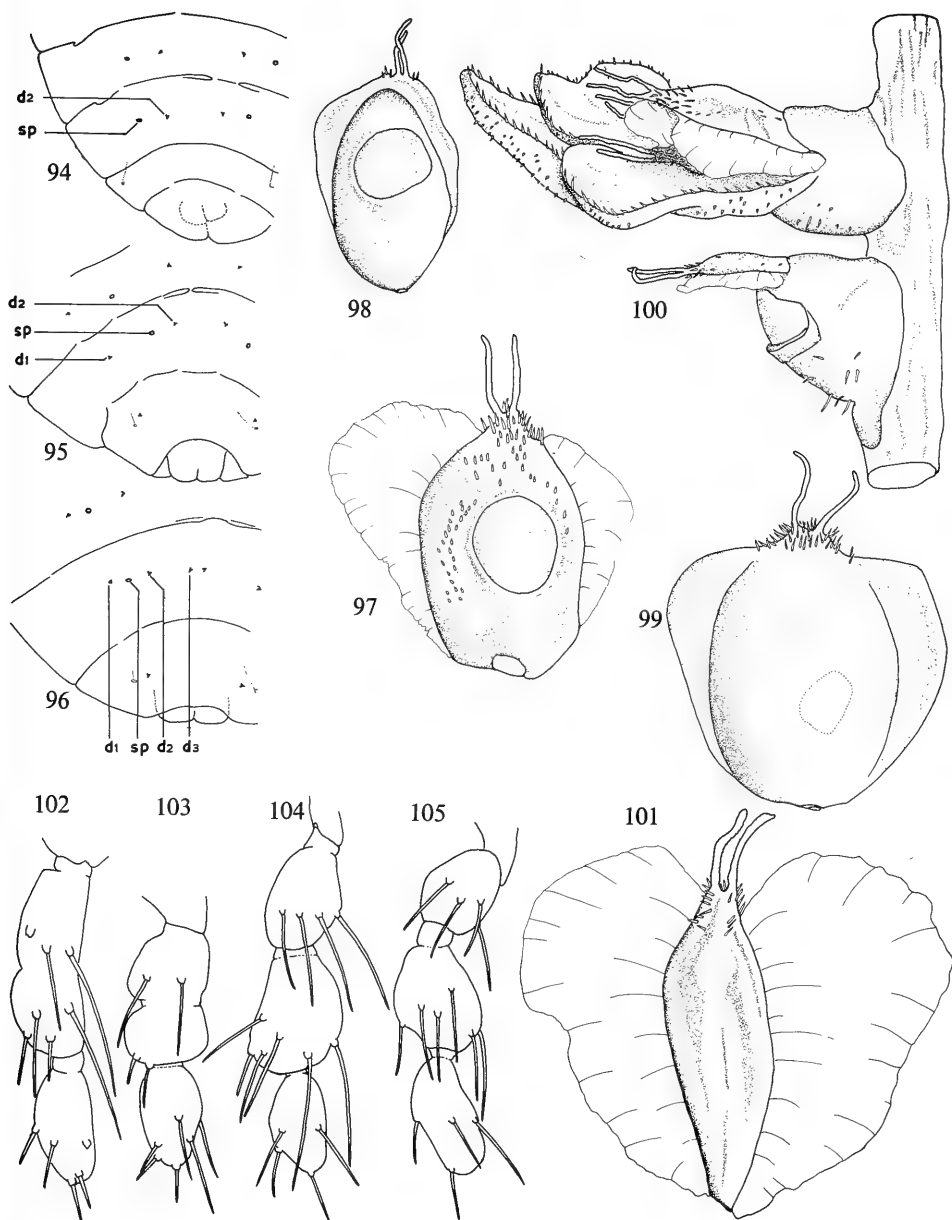


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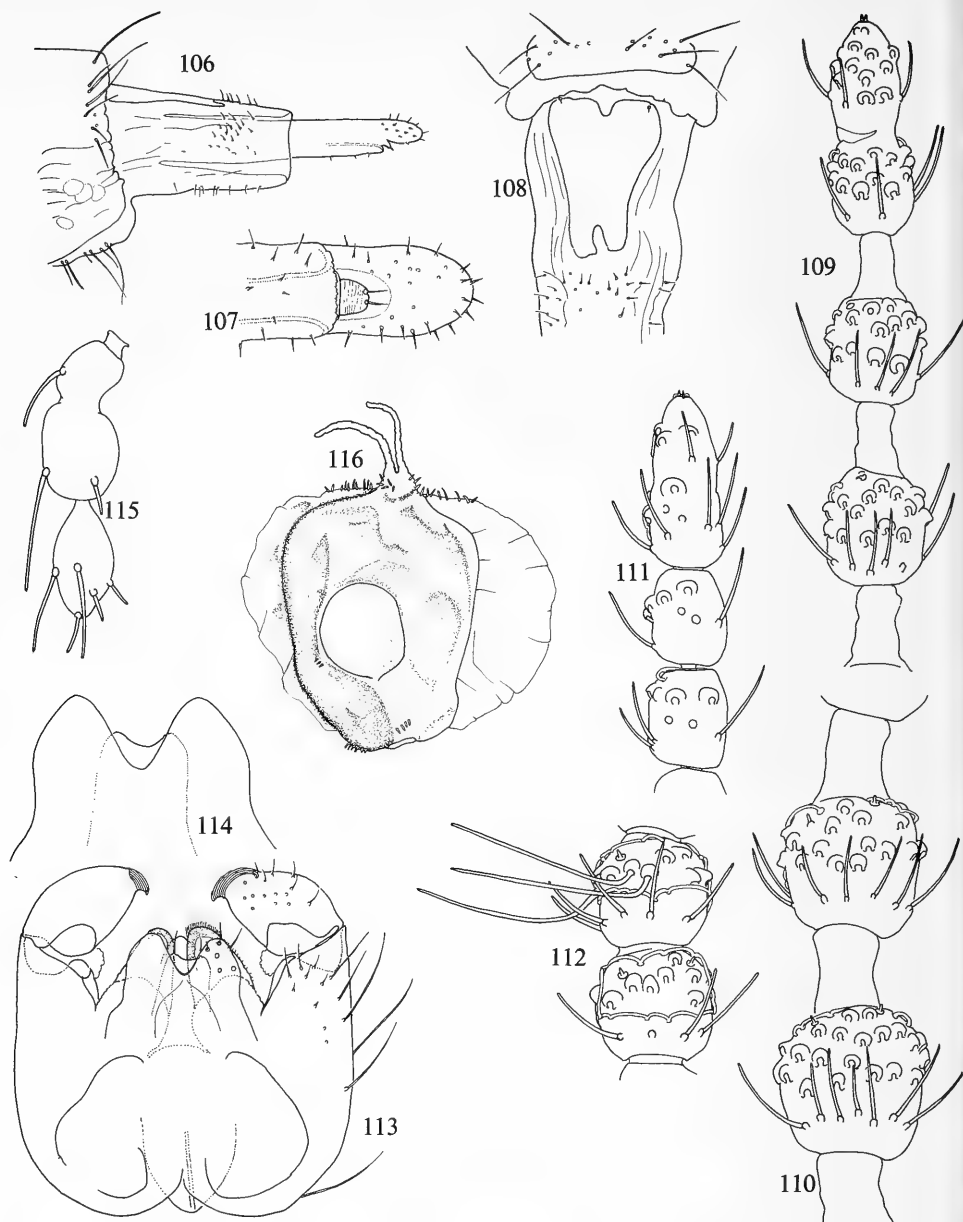
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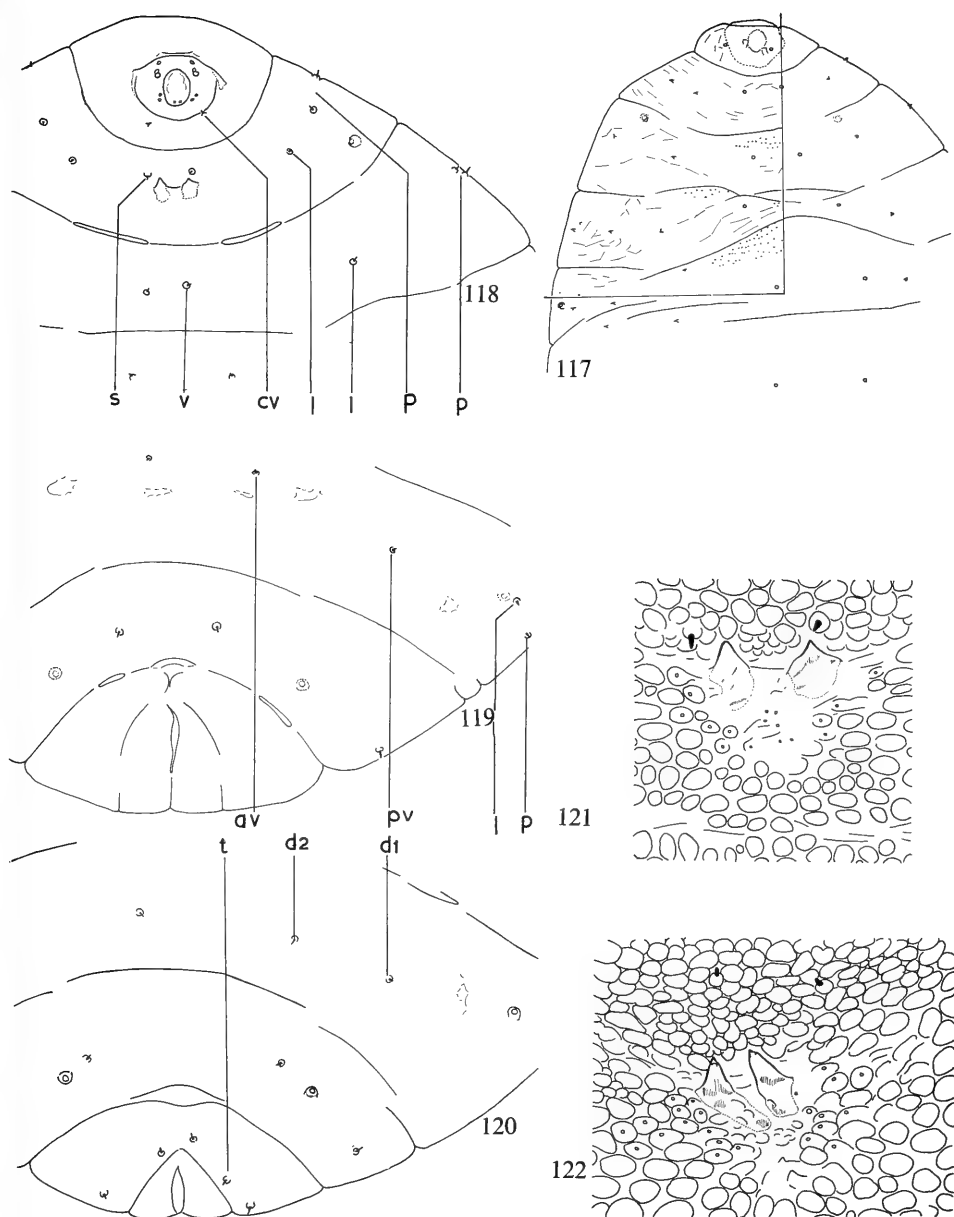
Figs. 88—93. *S. tarda*. 88, head and thorax of second instar, ventral aspect; 89, head, supernumerary segment and first thoracic segment of third instar, ventral aspect; 90, seventh and eighth abdominal segments and anal segment of third instar, ventral aspect; 91, ditto, dorsal aspect; 92—93, spathula sternalis: 92, The Netherlands, Meyendei, 93, Japan, Sapporo. For explanation of symbols, see figs. 62—69. 88—91,  $\times 140$ , 92—93,  $\times 425$ .



Figs. 94—96, seventh and eighth abdominal segments of pupa, dorsal aspect; 97—100, gall; 101, healthy fruit of *Betula pendula*; 102—105, female maxillary palp: 94, 99, 104, *S. tarda*; 95, 97, 102, *S. betulae*; 98, 103, *S. brevipalpis*; 96, 100, 105, *S. skuhravae*. d1—3, dorsal papilla; sp, sensory-pore. 94—96,  $\times 75$ ; 97—101,  $\times 13$ ; 102—105,  $\times 400$ .



Figs. 106—116. *S. steenisi*. 106, ovipositor, lateral aspect; 107, detail of female superior and inferior lamella, ventral aspect; 108, female eighth tergum; 109, male ultimate antennal segments; 110, male fifth and sixth antennal segments; 111, female ultimate antennal segments; 112, female fifth and sixth antennal segments; 113, male genitalia, dorsal aspect; 114, detail of male superior and inferior lamella; 115, female maxillary palp; 116, gall. 106,  $\times 85$ ; 107, 114—115,  $\times 400$ ; 108,  $\times 120$ ; 109—112,  $\times 330$ ; 113,  $\times 220$ ; 116,  $\times 13$ .



Figs. 117—122. *S. steenisi*. 117, head and thorax of second instar, ventral aspect; 118, head, supernumerary segment and first thoracic segment of third instar, ventral aspect; 119, seventh and eighth abdominal segments and anal segment of third instar, ventral aspect; 120, ditto, dorsal aspect; 121—122, sphatula sternalis: 121, Canada, Br. Columbia, 122, U.S.A., Montana. For explanation of symbols, see figs. 62—69. 117—120,  $\times 140$ ; 121—122,  $\times 425$ .













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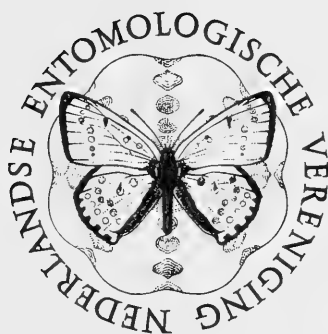
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# TIJDSCHRIFT VOOR ENTOMOLOGIE

UITGEGEVEN DOOR

DE NEDERLANDSE ENTOMOLOGISCHE VERENIGING



## INHOUD

K. VEPSÄLÄINEN and N. NIESER. — Life cycles and alary morphs of some Dutch *Gerris* species (Heteroptera, Gerridae), p. 199—212, figs. 1—2.



# LIFE CYCLES AND ALARY MORPHS OF SOME DUTCH *GERRIS* SPECIES (HETEROPTERA, GERRIDAE)

by

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With two figures

## ABSTRACT

Material of *Gerris* species was collected in the Netherlands during one summer, mainly of *G. odontogaster* (Zett.) and *G. lacustris* (L.), and less of *G. argentatus* Schumm. and *G. thoracicus* Schumm. Dutch populations are bivoltine like those in Central Europe.

*G. odontogaster* and *G. argentatus* are long-winged in the overwintering generation and alary dimorphic in the first new, midsummer generation. Non-diapause adults emerge during a period of one month, in mid July at the latest. The last overwintered adults die about mid July, non-diapause adults before the winter. Few eggs seem to be laid after mid August. The first new, overwintering diapause adults (macropters) emerge about 10 July, and a few younger instar larvae are still observed in September.

The life cycle of *G. lacustris* is similar to that of *G. odontogaster*, but short-winged adults also occur in the overwintering generation. There is a notable peak of short-winged imagos in midsummer and another peak in late summer. *G. thoracicus* is virtually long-winged throughout the year.

Evidence on colonization flights of midsummer non-diapause *G. lacustris* and *G. thoracicus* is given.

## INTRODUCTION

Andersen (1973), Vepsäläinen (1971, 1974a, 1974b) and Vepsäläinen & Krajewski (1974) have shown regularities in the relationship between the life cycles and alary polymorphism of European *Gerris* species (see also Järvinen, 1976).

1) *Odontogaster* type populations are univoltine and long-winged in northernmost Europe, and multivoltine (mostly bivoltine) and dimorphic over the main range of the species. Diapause is determined by shortening day lengths at the first four larval instars. Hence adults which have molted after mid July do not reproduce before the following spring. In northern Europe immediately reproducing (non-diapause) adults are short-winged, while diapausing adults are long-winged. In more southern populations the non-diapause group includes both short and long-winged individuals. Overwintering adults are long-winged.

2) *Lacustris* type populations are univoltine in northernmost Europe, and

bivoltine over the main range of the species. The populations are usually polymorphic through the year, although morph frequencies fluctuate. Diapause determination is as in *odontogaster* type populations. In northern bivoltine populations immediately reproducing adults are mainly short-winged; in southern populations both short and long-winged non-diapause individuals are found.

3) *Rufoscutellatus* and *najas* type populations are usually univoltine, and monomorphically long-winged or wingless, respectively.

The above grouping is a simplification of the highly varying life cycles in Finnish, Danish, Polish and Hungarian *Gerris* populations. For instance, the cycle of *G. thoracicus* in southernmost Finland is of the *odontogaster* type but Hungarian populations are, almost without exception, long-winged (Vepsäläinen, 1974a, 1974b). Moreover, dimorphic *G. najas* De Geer populations are also known (Poisson, 1957; Krajewski, 1969).

*G. odontogaster* and *G. lacustris* are distributed from northern Europe to the Balkans, *G. argentatus* and *G. thoracicus* reach northern Africa (for a survey of distributions, see Vepsäläinen, 1973). Diapause is thought to be an adaptation to adverse conditions, i.e. in winter, at least in most parts of Europe. Indeed, even in Faro, the extreme south of Portugal, the conditions in December are not favourable for larvae to reach adulthood. This is due to low food supply and low temperature. On the other hand, the autumn temperatures until November are comparable to cool summer days in the Netherlands and Denmark. So for southern populations a strategy with a longer reproductive season than in northern Europe could be possible. This could apply even to Dutch populations compared with Finnish, as in the Netherlands September is still quite warm, while in Finland it is often too cold for *Gerris* development. As in the northern hemisphere the days begin to shorten after summer solstice, about 22 June, diapause is determined all over the species ranges at approximately the same time. Therefore the mechanism of diapause determination may seem non-adaptive.

The purpose of the present work is to study the life cycles of Atlantic populations to reveal possible differences in the diapause reaction between these and northern and southern continental populations (Finland, Poland, Hungary). Simultaneously we report the alary morph frequencies, as the conditions of ponds and other small waters which are the main habitats of the *Gerris* species investigated may, on the average, be more stable and predictable in Atlantic than in continental climates. As a consequence Atlantic populations could maintain a higher frequency of midsummer short-winged adults than continental populations. The following are our results based on specimens collected in the Netherlands during 1974.

#### SITES STUDIED

The study area (ca. 200 km<sup>2</sup>) is located in the northern part of the Veluwe, prov. of Gelderland, with the village of Elspeet (52°17'N, 5°47'E) in its centre. The landscape is dominated by some rows of sandy hills formed by pleistocenic ice; one running approximately north—south from Nunspeet to Garderen. Most of our

sites are at the foot of these hills. Northwest of Heerde there is another chain of such hills, the Woldberg.

Most of the area has been planted with coniferous trees, but there are still a number of heathlands (e.g. the Speulderveld) and local stands of deciduous trees (e.g. near Nunspeet) left.

Except for those on the Speulderveld, the sampled sites are quite isolated, lying in small clearings in woods. With each locality description distances to nearest sites sampled are given. All these aquatic habitats were isolated from each other by land.

Our collecting sites are a subset of aquatic habitats of the Veluwe selected for zooplankton and later *Nepomorpha* studies, and supplemented with a collection of Speulderveld habitats. They were chosen in such a way that a maximal range of local *Gerris* habitats could be sampled. The following localities were included:

- N1, Nunspeet, Waskolk, about 1500 m<sup>2</sup>, surrounded by woods, isolated. Semi-aquatic vegetation (*Carex*, *Eleocharis*, *Juncus effusus*, *Glyceria* and *Sparganium*) at edges, from where most Gerridae were collected. Bottom: sand with a thin layer of plant debris, depth about 1 m. Used as a swimming pool during summer. Distance to N2, 4 km.
- N2, Nunspeet, Ossenkolk, about 1000 m<sup>2</sup>, surrounded by woods, isolated. Vegetation at edges *Eriophorum*, *Juncus bulbosus* and *Sphagnum*; pond filled with vegetation, mainly *Eleocharis*, *Juncus bulbosus*, *Sphagnum* and *Utricularia*. Bottom: sand with a thin layer of plant debris, depth for the greater part about 50 cm. Distance to N1, 4 km.
- N3, Ermelo, Speulderveld, *Carex rostrata* pool, about 100 m<sup>2</sup>, in open heath, bordered by *Molinia*, with *Carex rostrata* growing in the greater part of the pool. Bottom with a thick layer of plant debris, depth of free water 10-50 cm. Distance to N7-15, 20-300 m.
- N4, Garderen, Watergraafsmeertje, about 2500 m<sup>2</sup>, surrounded by woods, isolated. *Juncus effusus* and *Molinia* at edges; pond for the greater part filled with vegetation, mainly *Juncus bulbosus*, *Eleocharis multicaulis*, *Ranunculus* and *Scirpus*. Bottom: sand with a thin layer of plant debris, depth for the greater part about 20 cm. Distance to N3, 7-15, 6 km.
- N5, Heerde, pond at Buitenzorg, about 500 m<sup>2</sup>, surrounded by woods, isolated. Edges: sand and dry *Sphagnum*. For the greater part filled with vegetation, mainly *Sphagnum*. Bottom: sand with plant debris, depth about 50 cm. Distance to N6, 3 km.
- N6, Heerde, Kikkersgat, about 1000 m<sup>2</sup>, surrounded by woods, isolated. Edges with *Juncus bulbosus*, *Molinia*, *Rhynchospora*, *Scirpus* and *Sphagnum*; pond for the greater part filled with *Eleocharis multicaulis*, *Juncus bulbosus* and *Sphagnum*. Bottom with a thick layer of plant debris, depth about 50 cm. Distance to N5, 3 km.
- N7-10, Ermelo, Speulderveld, the four pits, 2 to 10 m<sup>2</sup>, on open heath, separated from each other by narrow dams, no water connections. Edges with *Calluna* and *Molinia*, pits partly filled with *Juncus bulbosus* and overhanging withered *Molinia*. Bottom: loamy soil with some plant debris, depth 5-80 cm. Distance to N3, N11-15, 20-300 m. The population of each pit: NE = N7, SE = N8, NW = N9, and SW = N10, has been studied separately.
- N11, Ermelo, Speulderveld, *Potamogeton* pit, 40 m<sup>2</sup>, edges with *Calluna*, pit for the greater part filled with *Potamogeton natans*. Bottom: loamy soil with plant debris, depth 10-100 cm. Distance to N3, N7-15, 20-250 m.
- N12, Ermelo, Speulderveld, *Utricularia* pit, 5 m<sup>2</sup>, on open heath, edges and bottom open sand with plant debris, a few *Utricularia minor* in the pit. Depth 5-25 cm. Distance to N3, N7-15, 10-250 m.
- N13, Ermelo, Speulderveld, *Juncus articulatus* pool, 20 m<sup>2</sup>, on open heath, edges with *Calluna* and *Juncus articulatus*, pool for the greater part filled with *Juncus bulbosus*. Bottom: sand with plant debris, depth about 20 cm but on 26.VI. it was without water, the bottom still wet; it is not known how many days the habitat was dry. Distance to N3, N7-15, 30-200 m.
- N14, Ermelo, Speulderveld, *Salix* pond, 60 m<sup>2</sup>, surrounded by *Salix* shrubs and some *Typha*; pond for the greater part filled with *Potamogeton natans* and some *Juncus bulbosus*. Bottom: loamy soil with plant debris, depth about 1 m. Distance to N3, N7-15, 15-300 m.

N15, Ermelo, Speulderveld, *Typha* pond, about 200 m<sup>2</sup>, Gerridae collected in a corner overgrown with *Typha*, about 20 m<sup>2</sup>. Bottom: sand with much plant debris (mainly from *Typha*), depth about 20 cm. Distance to N3, N7-14, 15-300 m.

## METHODS

The 15 populations were studied, and the larger populations partially collected, every second week from 16 May to 4 September 1974, N1-6 already on 16-19 April. Predominantly adults were collected, but larvae of the fourth and fifth instars were also taken to confirm reproduction. Occasionally younger larvae were included. During sampling the sites were checked for the occurrence of first and second instar larvae to estimate when the last eggs were laid. Unfortunately, samples were not taken after 4 September when egg-laying perhaps still continued on some of the sites.

Adults were classified according to wing length (short wings or wingless as against long wings). Notes were made on age (on basis of hardening and pigmentation grade of the chitin), colour of the female venter, stage of maturation (ovarian and testis), presence of adipose tissue, pigmentation of the mesoalutotum, and developmental stage of indirect flight muscles. When this information is combined, it is possible to make a reliable study of the life cycles. Details and reasons for the classification outlined here are given by Andersen (1973) and Vepsäläinen (1974a, 1974b).

## Habitat classification

The sites mentioned above were grouped for habitat features according to Vepsäläinen (1973) and showed little diversity (table 1). Shore vegetation was either sparse or moderately dense, the water surface was totally or moderately exposed to sunshine, and all ponds were stagnant and in late May over 10 cm deep. Plant coverage on water surface was mostly moderately to very dense, and showed in five cases a temporal change from scarce or moderate to dense. Two times the succession was reversed.

One site was classified as permanent (risk of drying up negligible), seven as semi-permanent (risk of drying up small), and seven as temporary (likely to dry up during exceptionally prolonged hot periods, i.e. at least once in some 50 years). In one semi-permanent and four temporary ponds depth of water had decreased under 10 cm by 26 June. One site (N13) was dry on 26 June but again contained water during the visit on 10 July.

## RESULTS

### Species numbers and habitats

Codes of each collecting site with habitat and species data are summarised in table 1. The number of species (apart from *G. rufoscutellatus*) per site varies between two and four (table 2). Permanent and semipermanent habitats (combined) tend to harbour more species than temporary ones ( $P=.025$ , one-tailed



Table 1. Sites studied, their habitat classification (see Vepsäläinen, 1973) and the recorded species. For the first three categories 1 means none or little, 2 = moderate, 3 = much. For permanency, 3 means temporary (\* dry on 26 June), for water movement 1 = stagnant, and for depth 2 = at least 10 cm and 1 = less than 10 cm. If two habitat classifications are given, the first refers to early summer (usually 30 May) and the other to midsummer (usually 26 June; in parentheses). Recorded species are shown with +, not recorded with —; the first sign refers to the adults, the second one to the fourth and fifth instar larvae.

Site code	Shore veget.	Exposition of the site	Plant coverage on water surface	Permanency	Water movem.	Water depth	la	od	ar	th	gi	ru
N 1	2	1	2	1	1	2	+	+	+	+	—	—
N 2	2	2	2(3)	2	1	2	+	+	+	+	—	—
N 3	2	1	2	2	1	2(1)	+	+	—	+	—	—
N 4	2	2	2(3)	2	1	2	+	+	+	—	—	—
N 5	1	2	2(3)	2	1	2	+	+	+	—	—	—
N 6	2(1)	1	1(3)	2	1	2	+	+	+	+	+	—
N 7	1	1	1(3)	3	1	2	+	+	—	—	—	—
N 8	1	1	2(1)	3	1	2(1)	+	+	—	—	—	—
N 9	1	1	2	3	1	2(1)	+	+	—	—	+	—
N 10	1	1	2	3	1	2	+	—	—	+	—	—
N 11	1	1	3	3	1	2(1)	+	—	—	+	—	—
N 12	1	1	1(2)	3	1	2(1)	+	+	—	—	+	—
N 13	2	1	1	3*	1	2*	+	—	—	+	+	—
N 14	1	2	3	2	1	2	+	+	+	—	+	—
N 15	2	1	2	2	1	2	—	—	+	—	—	—

Table 2. Number of species per habitat grouped for permanency.

Habitat	number of species	2	3	4
Permanent				1
Semi-permanent		1	1	5
Temporary		3	2	2

Mann-Whitney U-test; the null hypothesis is that the temporary habitat has the same distribution over species numbers as the more permanent habitat group).

Notably *G. argentatus* seems to prefer (semi-)permanent habitats, being absent only from one semi-permanent, but all temporary, habitats. *G. lacustris* seems to be indifferent to this habitat feature. For the remaining species the data are inconclusive.

### Life cycles and alary morphs

We will try to give a general picture of wing length variation and life cycles in Dutch *Gerris*. Hence we have summed the information from all 15 localities in figs. 1 and 2. There are probably differences between populations (see Vepsäläinen, 1974b: 12-13) but our material is too scarce to reveal any.

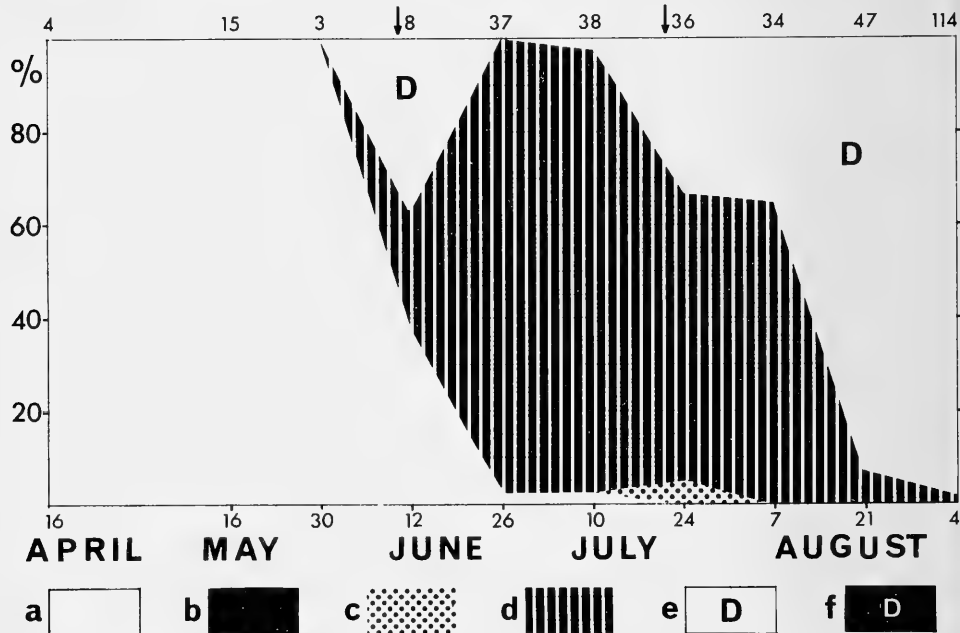


Fig. 1. Seasonal changes in the proportions of the different female forms of *Gerris odontogaster*. The numbers of females per sampling day are given above. The diagram is an approximation based on dissected material of 84.4% of the micropter and 44.1% of the macropter females. The arrows above indicate the first and last samples, respectively, where about newly emerged non-diapause females were found. a) hard chitin, dark venter, eggs or maturing oocytes, macropter; b) as a but short-winged; c) pale venter, eggs or maturing oocytes, macropter; d) as c but short-winged; e) dark venter, immature, macropter; f) as e but short-winged.

*Gerris odontogaster*

The overwintering population is long-winged. The first fifth instar larva was captured on 30 May. First short-winged adults were caught on 12 June and short-winged individuals dominated from late June to early August. The specimens in the late August and early September samples were almost all long-winged (fig. 1, table 3).

The short-winged adults are classified as micropters, wing length usually varying from 1 to 2 (see Vepsäläinen, 1974b, fig. 1). On 24 July, one male with wing length 3.5 (i.e. brachypterous) was collected (incompletely pigmented; age less than one week). The midsummer micropters are non-diapausing individuals whose gonads mature soon after the final moult. One to two weeks old micropterous females usually have full-sized eggs. Some non-diapause macropters emerge simultaneously with micropters. Both non-diapause female types are usually easy to distinguish from overwintered and diapause females by their pale venters in otherwise completely pigmented individuals. Males, however, are almost without exception dark below (for details, see Vepsäläinen, 1974a).

Diapause individuals with dark venter begin to emerge about 10 July, and gradually this group replaces other groups. The last two non-diapause females, which have been classified as semi-soft (refers to the hardening of the chitin), were captured on 24 July. As the hardening of the chitin may take over two weeks after the final moult, it can be estimated that the ecdysis has taken place about mid July. After 24 July all soft or semi-soft females checked for maturing oocytes have been in diapause. The mature, late summer females are older individuals, which have already laid most egg batches and die before the winter.

On 4 September no young larvae (first to third instars) were observed on eight

Table 3. Fraction of short winged specimens for males and females in *G. argentatus* (apteres), *G. lacustris* (mainly brachypters) and *G. odontogaster* (micropters) with *s* (standard deviation in sample) and, between brackets, *n* (the number of specimens in sample) over all habitats on the various sampling days. Actually sampling took place on two consecutive days, of which the first is mentioned.

	<i>G. argentatus</i>		<i>G. lacustris</i>		<i>G. odontogaster</i>			
	sexes pooled		♂	♀	♂		♀	
date								
16.IV	0	( 5)	0.07±0.07 (14)	0.10±0.10 (10)	0	(11)	0	( 4)
16.V.	0	(18)	0.06±0.04 (32)	0.10±0.05 (42)	0	(12)	0	(15)
30.V.	0	( 3)	0.11±0.06 (28)	0.32±0.09 (28)	0	( 1)	0	( 3)
12.VI.	0	( 5)	0.25±0.15 ( 8)	0 (10)	0	( 4)	0.38±0.17 ( 8)	
26.VI.	0.75±0.22 ( 4)		0.47±0.13 (15)	0.67±0.10 (24)	0.96±0.04 (23)		0.97±0.03 (37)	
10.VII.	1	(12)	0.42±0.08 (36)	0.41±0.08 (44)	0.73±0.10 (22)		0.95±0.04 (38)	
24.VII.	0.80±0.18 ( 5)		0.27±0.06 (49)	0.29±0.07 (49)	0.74±0.10 (19)		0.61±0.08 (36)	
7.VIII.	0.39±0.14 (13)		0.12±0.04 (67)	0.15±0.05 (65)	0.64±0.13 (14)		0.65±0.08 (34)	
21.VIII.	0	(11)	0.17±0.07 (30)	0.41±0.10 (27)	0.04±0.03 (47)		0.06±0.04 (47)	
4.IX.	0	(29)	0.49±0.08 (39)	0.50±0.09 (32)	0.02±0.02 (65)		0.01±0.01 (114)	

sites, and in seven populations they were very few or few. The species could not be identified in the field. On 21 August four populations had still "quite a number" of young larvae.

The one macropterous male checked for testis maturation on 7 August still had soft chitin (hence it was not over a week old) and well-developed testes. It is not known which proportion of late summer males has well developed testes nor whether they actually copulate in late summer.

Histolysing indirect flight muscles were already found on 16 April in overwintered females with developing oocytes, and totally histolysed ones in females with eggs on 16 May. Micropters have undeveloped flight muscles, but non-diapause as well as diapause macropters develop indirect flight muscles in approximately two to three weeks in nature. It seems that an individual with the combination of characteristics — fully pigmented, semi-hard, mesoalinetum III or perhaps II (for the classes, see Andersen, 1973, fig. 10), and indirect flight muscle fibres with a diameter of 35-50  $\mu\text{m}$  — is already capable of flight.

Adipose tissue was found in individuals with undeveloped gonads. Non-diapause individuals did not have adipose tissue; this was also the case with the micropterous female with eggs, collected on 4 September.

In the following we list some exceptions from the above life history picture. In the 12 June samples we found one semi-soft/semi-hard (hence not overwintered), fully pigmented, dark-ventered female with undeveloped oocytes, and one semi-soft, almost fully coloured female with dark venter and undeveloped oocytes (both macropterous). Usually the oocytes of new-generation females which develop in early summer are already well maturing in fifth larval instars (e.g. Andersen, 1973, fig. 7).

In the 10 July sample there was one semi-hard, completely pigmented, macropterous female with light venter but totally undeveloped oocytes (mesoalinetum II and diameter of indirect flight muscle fibres about 30  $\mu\text{m}$ ).

Collected on 26 June, there is one light-ventered micropterous female with abnormal intestine and no eggs, and on 10 July, one semi-soft, light-ventered micropterous female with contents of abdomen "rotten".

One micropterous male, collected on 24 July, had asymmetrical wings, one hemielytron being longer and deformed.

Sex ratio was female weighted (39.5% males,  $n=554$ ,  $P<.001$ ; .95 confidence limits for fraction of males .36-.44). The deviation is a sum effect of both midsummer micropters and late summer diapause macropters. (Heterogeneity  $\chi^2_{(7)} = 13.60$ ,  $.10 < P < .05$ ; with the null hypothesis of even sex ratio in the samples. The heterogeneity of the whole material (early summer included) is statistically significant:  $\chi^2_{(11)} = 24.32$ ,  $P < .025$ ). Significant heterogeneity indicates a shift in sex ratio during the cycle.

### *Gerris argentatus*

The number of specimens is small, 105 imagoes in all. The general picture is like that in *G. odontogaster* (table 3). The overwintering population is long-winged, the

midsummer one dimorphic. The short-winged individuals are mostly apterous but sometimes micropterous. On 10 July one newly emerged male with hemielytra 6+ and hind wings 4+ (brachypterous) was taken.

In this species also a few long-winged, non-diapause adults occur together with apters: one macropterous female on 7 August had completely hardened chitin, light venter and full-sized eggs.

Midsummer non-diapause females differ from diapause females by their more or less light venter. However, Dutch *G. argentatus* females are usually notably darker than the equivalent type in *G. odontogaster* (the former as the pattern *argentatus* D' and the latter as B' or C' *odontogaster* in fig. 3, Vepsäläinen, 1974a). No differences have been noticed in the ventral coloration between non-diapause short- and long-winged females.

The last overwintered adult (with strongly histolysed indirect flight muscles) was collected on 26 June. The first new generation apters were taken on the same day, and the first fifth instar larva on 12 June. No soft non-diapause individuals were collected after 10 July, and the first diapause macropters were not taken before 7 August. (On 24 July only five adults were captured.)

Indirect flight muscle histolysis was noted from 16 April onwards in overwintered individuals. In late summer, diapause imagoes had well-developed indirect flight muscles and voluminous adipose tissue.

The fraction of males was 50% ( $n=105$ ).

### *Gerris thoraċicus*

In this species no definite evidence of alary dimorphism was obtained. The collected 61 imagoes were macropters with the exception of one male brachypter in the 10 July sample.

The Dutch population, like in the two previous species, is bivoltine (at least partially). The first fifth instar larva was captured on 12 June, and the first new, non-diapause imagoes (1 ♂ 3 ♀) on 26 June. The last overwintered specimen (1 ♂) was caught likewise on 26 June. The last young non-diapause imago was obtained on 10 July, and the first records of diapause individuals are from 24 July (two semi-hard young individuals, one of which had reached stage IV mesoalnotum coloration). The last female with eggs occurred on 21 August.

*G. thoraċicus* differs from the previous two species in that both diapause and non-diapause individuals are nearly entirely dark below. The ventral coloration is therefore not indicative of a reproductive stage.

Another difference with the preceding species is evident: usually, histolysis of indirect flight muscles does not take place in overwintered *G. thoraċicus*. In the last overwintered specimen (1 ♂ on 26 June) indirect flight muscles were still full-sized.

The one brachypterous male (semi-hard, totally pigmented, hemielytra 7.2, hind wings 5.2; called submacropter by many previous investigators) had well developed testes but undeveloped flight muscles.

The fraction of males was 46% ( $n=61$ ).

*Gerris lacustris*

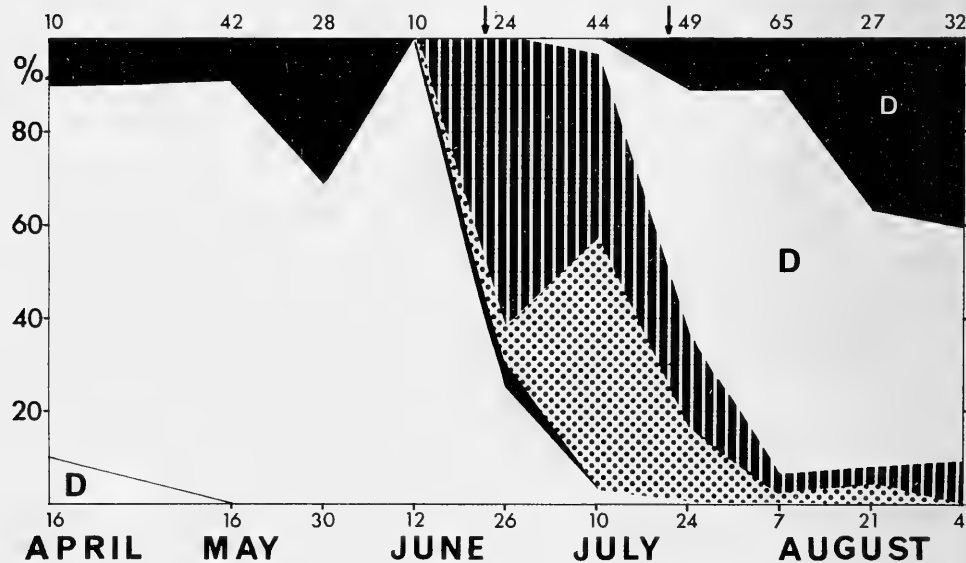
This species has a more complicated life cycle as even the overwintering population is polymorphic. A notable peak of brachypters (the other morph in this species, medially short wings) occurs in midsummer. Later the relative frequency of brachypters declines to rise again in the early September sample. In late spring brachypter frequencies are at the lowest (fig. 2, table 3).

The high frequencies of brachypters in mid summer are explained by the fact that a higher proportion of the non-diapause imagoes are short-winged (fig. 2). The situation is analogous with *G. odontogaster* and *G. argentatus* which have a mid-summer short-winged, non-diapause group, except that *G. lacustris* populations also include overwintering brachypters.

The first fifth instar larva was captured on 12 June, and the first new, non-diapause adults (both brachypters and macropters) on 26 June. The last overwintered imago (one brachypterous female) was caught on 10 July.

The last young, definitely non-diapause adult (a brachypterous female), incompletely pigmented and semi-soft, with the largest oocytes at least 860  $\mu\text{m}$ , was captured on 10 July. However, still on 24 July one brachypterous female, soft and incompletely pigmented (signs of darkening venter could be traced), still had oocytes of 550  $\mu\text{m}$  maximum length. Furthermore, on the same day one semi-soft and incompletely pigmented brachypterous female (with signs of dark venter) with maximal oocyte length of 480  $\mu\text{m}$  was caught. These two oocyte measurements lay at the lower boundary of the class "maturing" of Andersen (1973: 500  $\mu\text{m}$ ) but

Fig. 2. Seasonal changes in the proportions of the different female forms of *Gerris lacustris*. Symbols as in fig. 1 but instead of dark (light) venter read dark (light) thoracic venter. The diagram is an approximation drawn on basis of 60.6% of the brachypter and 42.2% of the macropter females.



considerably exceed the 240  $\mu\text{m}$  used by Vepsäläinen (1974a) in routine scrutiny. It is not clear whether these two females really were diapausing or not. The coloration of the thoracic venter indicates diapause (accordingly a later resorption of oocytes is to be expected). The colour of the venter is, however, only a good working guide, as in the same samples there is one semi-hard, ventrally dark (only sternites 6 and 7 medio-apically light) brachypterous female with eggs. In this case there could not be any question of an overwintered adult as the ventral coloration was still partially brown-black (a sign of ongoing pigmentation). Another puzzling individual is the macropterous female caught on 7 August, which was incompletely pigmented, semi-soft/semi-hard and had only one, 365  $\mu\text{m}$  long oocyte in its otherwise undeveloped ovaries.

Thus it is clear that whether the females were classified as maturing by the criterium of minimum oocyte length of 240  $\mu\text{m}$  or 500  $\mu\text{m}$ , it is preferable to check for additional signs of diapause in border cases as well. The positive correlation between reproductive activities and poorly developed adipose tissue, and diapause and well-developed adipose tissue seems to hold true in individuals which have attained at least semi-hard chitin, but is poorly developed in soft and semi-soft imagoes, even if completely pigmented.

Non-diapause adults were still found in late August and early September, although the numbers were low. The first diapause imago occurred on 10 July, and on 24 July diapause imagoes dominated in the total material.

The positive relation between a light thoracic venter and a non-diapause state in *G. lacustris* is good in our Dutch material. Only one possible exception (above) was found. Moreover, at least four macropterous females were seen (on 24 July), in which the general impression was all-dark. A closer inspection revealed that in all these individuals the pattern of lighter non-diapause adults could be seen. The coloration was only more grey-brown than usually ("smoky"), but still contrasted against the black areas of the thoracic venter. The coloration was much the same as in the non-diapause type of *G. paludum* F. in fig. 3 by Vepsäläinen (1974a).

Brachypterous *G. lacustris* adults have undeveloped flight muscles. Diapause macropters develop functional muscles, which, after overwintering, are histolysed. In our Dutch material we already have macropterous females with histolysing muscles on 16 May. In mid summer, diapause imagoes seem to reach flight ability in about two weeks or shorter: two females collected on 24 July were semi-hard, totally pigmented, with mesoalinetum II and the diameter of indirect flight muscle fibres 30-50  $\mu\text{m}$  and 32-45  $\mu\text{m}$ , respectively.

Sex ratio of brachypters is perhaps female-weighted (43% males,  $n=174$ ,  $P=.07$ ); in macropters the male percentage is 51 ( $n=475$ ).

### Other species

Altogether 23 *G. gibbifer* Schumm. adults (10 ♂, 13 ♀) were collected, all macropters (one female with hemielytra 7.8 and hind wings 7.0-7.1). The first new generation adult was caught on 26 June; it was a semi-soft female with undeveloped oocytes. Oocyte maturation could not be detected in an already

semi-hard/hard female on 10 July. Thus the voltinism of Dutch *G. gibbifer* cannot be determined on the basis of our material.

Only two observations of overwintered *G. rufoscutellatus* Lat., probably the same female, were made: on 30 May, and 12 June, when its abdomen was swollen with eggs. No larvae were found.

### Midsummer colonization flights

Usually little can be said about colonization flights without marking-recapture work. The temporary drying up of pond N13 (dry on 26 June, water on 10 July), however, gave some information.

On 26 June the bottom and the bordering vegetation were checked for *Gerris*: none were found. On 10 July one *G. thoracicus* macropterous male and one *G. lacustris* macropterous female (semi-hard, light thoracic venter, eggs; thus a midsummer, non-diapause adult) were collected. On 24 July another *G. thoracicus* macropterous male and *G. lacustris* macropterous female (semi-hard, light thoracic venter, eggs, totally pigmented mesoalutotum and well developed indirect flight muscles) were taken.

On 7 August two fifth instar larvae of *G. gibbifer* and three *G. thoracicus* females were netted. The *G. gibbifer* larvae may have developed from eggs which survived the drought, as on 30 May and 12 June there was a *G. gibbifer* female in the pond. Of the *G. thoracicus* females, two had eggs and the third was in diapause. As no *G. thoracicus* larvae were collected from N13, it is improbable that the adults had developed there.

Accordingly, colonization flights of mid summer reproducing *G. lacustris* and *G. thoracicus* do occur. Earlier straight evidence is rare. Fernando (1959) reports one immigrant *G. odontogaster* female which produced offspring. Here the female was fertilised before the migration, as perhaps, were some females of our immigrants to population N13. There seems to be a clear difference therefore in the stage of maturation between colonising overwintered and colonizing midsummer females, as spring migrants have undeveloped or very poorly maturing oocytes (Landin & Vepsäläinen, 1977).

### DISCUSSION

The life cycles and wing lengths of the studied *Gerris* species are by and large similar to those in Poland (Vepsäläinen & Krajewski, 1974) and Hungary (Vepsäläinen, 1974a). The Dutch populations differ, however, in these respects from more northern ones in Finland (see Vepsäläinen, 1974b). Admittedly, there are more non-diapause macropters in the mid-summer generation in Hungary (and, considering *G. lacustris*, also in Poland). This could reflect the higher degree of temporariness of more southern and continental pond habitats.

The diapause of Dutch *Gerris* seems to be fixed at about the same date, and presumably by the same mechanism, as that of Finnish, Polish and Hungarian populations (for a generalized model, see Vepsäläinen, 1974c: fig. 2).

In northern Europe early winter understandably favours diapause determination



by decremental changes of day length. On the average the potential reproductive season is longer and the risks of drying up of population sites are smaller in Atlantic climates than in continental ones at the same latitudes. Thus it could be assumed that in Dutch populations selection would operate towards a later termination of reproductive activities. This could be achieved in at least two ways: by later onset of diapause and/or longer life span of the midsummer, non-diapause adults.

Usually the diapause of insects is determined by the absolute lengths of daily illumination period (Danilevskii, 1965) but in *Gerris* the change of length is critical: shortening day lengths determine the diapause. Thus it is not easy to postpone the onset in diapause in *Gerris*. The associated genetic changes would have to be radical, and would be possible only in effectively isolated populations under strong selective pressure. The Dutch populations in this respect are not submitted to strong natural selection and are insufficiently isolated. From the degree of temporariness of our study ponds it can be presumed that gene flow between local *Gerris* populations is notable, which is in agreement with the general views on migration strategies of the denizens of more or less temporary habitats (e.g. Southwood, 1962; Dingle, 1974; Vepsäläinen, 1974b). Even long range flights are known (Leston, 1956). These tend to swamp the effects of local selection pressures. Moreover, a recent simulation study on *Gerris* populations (Järvinen & Vepsäläinen, unpublished) showed that even in the absence of imminent threat of unfavourable conditions it may sometimes (e.g. in habitats of low productivity) be advantageous to limit the number of successive generations.

The strategy to postpone the end of reproductive activities by cutting down the mortality of the midsummer non-diapause adults is likely to work in *Gerris*. Unfortunately we lack Dutch data on last first-instar larvae in autumn. Consequently, nothing can be said of the approximate last day of egg-laying of Dutch *Gerris*. Here would be an important field of study: to work out the length of the reproductive season in terms of last egg-laying dates of *Gerris* species in different parts and climates of the western Palaearctic. The theoretical value of such a study is evident, as the onset of diapause seems to occur about the same date everywhere irrespective of the widely differing lengths of the potential reproductive season.

Another point of discussion comes from our observation of two completely pigmented new-generation *G. odontogaster* females (semi-hard and semi-soft) with dark venter and undeveloped oocytes, captured on 12 June. The observed features together are a reliable sign of diapause. Vepsäläinen (1974d) obtained such laboratory offspring of Finnish *G. odontogaster* which were reared in short, lengthening illumination. The applied laboratory days were shorter than Finnish late instar larvae can meet in nature in early summer. Such females are expected to be very rare in natural populations, as the selection pressures are heavy against diapause behaviour in early summer. It cannot, however, be ruled out that oocyte maturation both in the Finnish laboratory reared and the Dutch females was only retarded and would have started later in somewhat longer days, producing exceptionally new-generation females with eggs, though with dark venter. Such individuals have very rarely been observed (e.g. Vepsäläinen & Krajewski, 1974, in

*G. lacustris*). We presume that retarded maturation instead of real diapause is the more likely explanation in some individuals which develop in short, lengthening days — i.e. exceptionally early in summer — in nature.

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## INHOUD

F. WILLEMSE. — Classification and distribution of the Sexavae of the Melanesian Subregion (Orthoptera, Tettigonioidea, Mecopodinae), p. 213—277, text-figs. 1—7, pls. 1—18.





CLASSIFICATION AND DISTRIBUTION OF THE SEXAVAE  
OF THE MELANESIAN SUBREGION (ORTHOPTERA,  
TETTIGONIOIDEA, MECOPODINAE)

by

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With 7 text-figures and 18 plates

ABSTRACT

An attempt is made to classify the species of the genera *Sexava* Walker, *Segestes* Stål and *Segestidea* Bolívar on the basis of previously not used characters, such as the venation of the fore wing and the morphology of the male stridulatory apparatus.

The following new synonyms and new combinations are proposed: *Eumossula* C. Willemse, 1957 = *Segestidea* I. Bolívar, 1903; *Segestidea gracilis* (C. Willemse, 1957), comb. nov. (from *Eumossula*); *Segestes grandis* C. Willemse, 1955 = *Sexava coriacea* (Linné, 1758); *Sexava femorata* C. Willemse, 1940 = *Segestidea princeps* I. Bolívar, 1903 = *Segestidea novaeguineae* (Brancsik, 1897), comb. nov. (from *Moristus*); *Segestidea hanoverana* C. Willemse, 1957 = *Segestidea leefmansi* (C. Willemse, 1940), comb. nov. (from *Sexava*); *Segestidea insulana* C. Willemse, 1957 = *Segestidea uniformis* (C. Willemse, 1940), comb. nov. (from *Sexava*); *Segestidea acuminata* (Kästner, 1934), comb. nov. (from *Segestes*); *Segestidea rufipalpis* (C. Willemse, 1966), comb. nov. (from *Sexava*). Besides the following new taxa are described: *Segestes stibicki* sp. n., *Segestes cornelii* sp.n., *Segestes brevipennis* sp.n., *Segestidea gracilis simulatrix* ssp.n. and *Segestidea marmorata occidentalis* ssp.n.

Keys to the taxa and distribution maps are given. The range of the species and subspecies is now in agreement with the general zoogeography of the area concerned; previous records proved to be partly erroneous.

CONTENTS

Introduction	213
Material and acknowledgements	214
Generic and specific characters in Sexavae	215
Key to the genera	218
<i>Sexava</i> Walker	218
Key to the species of <i>Sexava</i>	219
<i>Segestes</i> Stål	227
Key to the species of <i>Segestes</i> from New Guinea and Bismarck Archipelago	230
<i>Segestidea</i> Bolívar	240
Key to the species of <i>Segestidea</i>	241
References	256
Index	277

INTRODUCTION

The species of the genera group *Sexava* Walker, *Segestes* Stål and *Segestina* I. Bolívar are large katydids, called “coconut treehoppers” by entomologists. Some

of them have been reported as important pests of coconut trees in the Moluccas, New Guinea and the Bismarck Archipelago.

Dr. J. L. Stibick of the Department of Agriculture, Stock and Fisheries, Konedobu, Papua, has sent me material for identification since 1971. It came out that the taxonomy of this group of genera was considerably confused and generic distinction was not well understood. As a result, some species were described twice, in different genera.

The range of the species of the Sexavae covers the Philippines, Celebes, the Moluccas, New Guinea and the Bismarck Archipelago. The present study deals mainly with species occurring in the Melanesian Subregion.

Only the more important taxonomic references are mentioned. A more extensive, although incomplete, bibliography can be found in Beier (1966: 311—316). The measurements given throughout the text concern the lengths and are in millimeters. The nomenclature of the wing venation is that given by Ragge (1955). Figures of the male stridulatory apparatus and abdominal terminalia of the taxa of each genus are nearly on the same scale, those of the whole insects not. On the distribution maps, only reliable localities are indicated, while a few previous records are omitted as no material was at hand and identification appears doubtful.

#### MATERIAL AND ACKNOWLEDGEMENTS

Depositories of types and other material are given in abbreviated form throughout the text, as follows:

ANSP	Academy of Natural Sciences, Philadelphia;
BMNH	British Museum (Natural History), London;
BPBM	Bernice P. Bishop Museum, Honolulu;
CAS	California Academy of Sciences, San Francisco;
CW	Willemse's collection, partly Natuurhistorisch Museum, Maastricht, partly author's address;
DASF	Department of Agriculture, Stock and Fisheries, Konedobu, Papua;
IEM	Instituto Español de Entomología, Madrid;
ITZ	Instituut voor Taxonomische Zoölogie, Amsterdam;
NMB	Naturhistorisches Museum, Basel;
NMW	Naturhistorisches Museum, Wien;
NR	Naturhistoriska Riksmuseet, Stockholm;
NS	Naturkundemuseum, Stettin;
RNH	Rijksmuseum van Natuurlijke Historie, Leiden.

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## GENERIC AND SPECIFIC CHARACTERS IN SEXAVAE

The Sexavae, as understood by C. Willemse (1961: 93), refer to the "Sexava-Gruppe" of Karny (1924: 144) and Kästner (1934: 24) and comprise the genera: *Sexava* Walker, 1870, *Segestes* Stål, 1877, and *Segestidea* I. Bolyévar, 1903. Previously (Karny, 1924: 143; Kästner, 1934: 24), the name Sexavae was used in a much wider sense, covering also the Phrictae and Mossulae groups of genera. These three groups of genera are united under one of the two tribes recognized in the subfamily Mecopodinae, the Sexavini (called Moristini by Redtenbacher, 1892: 189; Segestini by Hebard, 1922: 176; Sexavae by Karny, 1924: 143, and Kästner, 1934: 24; Sexavinae by C. Willemse, 1961: 93; Sexavini by Beier, 1966: 305). Keys to the tribes and genera were given by Redtenbacher (1892: 189), Caudell (1916: 2), Karny (1924: 143, 147), Kästner (1934: 24, 32) and C. Willemse (1961: 93, 94, 107, 111). While the distinction between the Phrictae and the remaining genera of the tribe appears clear, that between the Mossulae and the Sexavae is more gradual and demands further study.

Distinction between the three genera of the Sexavae was based on the presence or absence of a posterior dorso-apical spine of the fore and mid tibiae, and the comparative measurements of body, fore wing, head and pronotum (Caudell, 1916: 3; C. Willemse, 1957: 42; 1961: 107). In *Sexava* and *Segestidea*, the apex of the fore and mid tibiae bears, at least at the posterior side, a small dorsal spine. This spine is not to be confused with one or more spines located more proximally on the dorsal margins of the tibiae. In *Segestes*, the dorso-apical spines are believed to be lacking. A study of the available material reveals that this character is indeed a reliable one, but that there are exceptions. In three out of 38 specimens assigned to *Segestes decoratus* Redtenbacher, dorso-apical spines of fore and mid tibiae are present. In these specimens the spines are sometimes very small and not uniformly present on all fore and mid tibiae. An explanation of these exceptions can be found in the remarkable stability of the occurrence of the dorso-apical spines in the subfamily. Actually, the presence of these spines has been used as a subfamily character as early as Brunner von Wattenwyl (1878: 10) until recently (Beier, 1955: 246; 1962: 2), although Redtenbacher (1892: 183) already gave comments on this point and re-defined the Mecopodinae. A renewed study of other *Segestes* material at hand, i.e. the remaining part of the material in the Vienna museum (Kaltenbach, in litt. 11.ii.1976) and of the type-species *vittaticeps* Stål, proves that the dorso-apical spines in that material are indeed lacking. Therefore it seems reasonable, in spite of the very few exceptions, to consider the presence or absence of dorso-apical spines of the fore and mid tibiae a character of generic significance.

The distinction between *Sexava* and *Segestidea*, as indicated previously, was arbitrary (Caudell, 1916: 3; C. Willemse, 1957: 42; 1961: 107). Among the characters mentioned, it was noted that the fore wing in *Sexava* is comparatively wider than in *Segestidea*, the venation not being mentioned. Also Redtenbacher, in his study on the wing venation (1886: 179, pl. 11 fig. 24), discussed the wings in *Moristus* (= *Sexava*), but omitted the true nature of its typical venation.

Comparison of the male fore wings of *Sexava*, *Segestidea* and *Segestes*, reveals

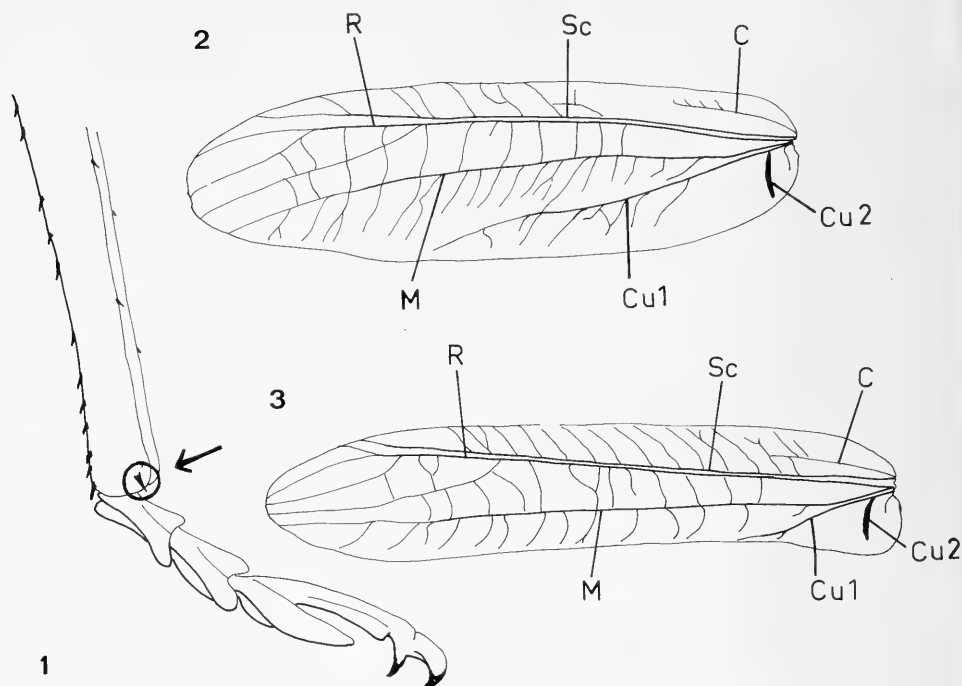


Fig. 1. *Segestidea*, right fore tibia and tarsus, posterior view. Figs. 2—3. Left male fore wing: 2, *Sexava coriacea* (L.); 3, *Segestidea novaeguineae* (Brancsik).

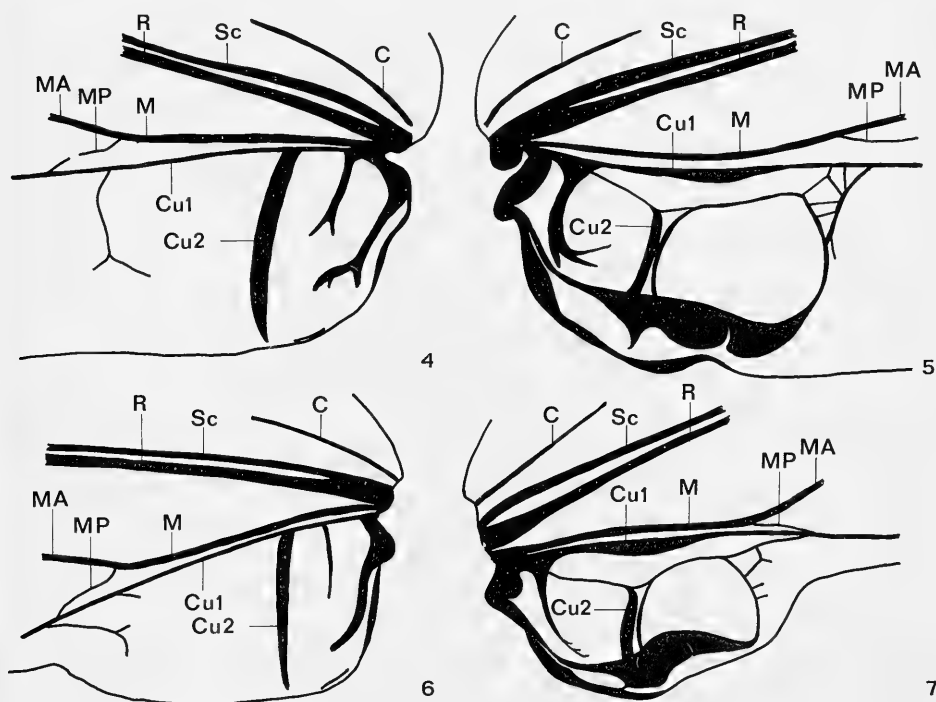
that the fore wings overlap each other basally over a short distance in *Segestidea* and *Segestes*, whereas in *Sexava* the overlap is conspicuous over most of their length. It proves that the course of the first cubital vein, Cu1 (which may fuse or not with the variably developed MP), in *Sexava* is remarkably different from that in both other genera. This character affects the stridulatory area of the male fore wing and is considered more reliable for a natural classification of species at generic level than previously used characters.

The flexed fore wing in the species of *Sexavae* is folded along Cu1. The result of this fold is to bring the areas behind Cu1 (cubital and anal areas) into a roughly horizontal position over the abdomen, the remainder of the wing being roughly vertical. In *Segestidea* and *Segestes*, Cu1 and its fold run obliquely to the hind margin of the wing, almost reaching the latter at a short distance from the wing-base (text-figs. 3, 6, 7). From there, Cu1 may more or less merge with the archdictyon or continue parallel but very close to the hind margin of the wing. Cu1 and its fold delimit a sharply defined triangular area at the wing-base. This area contains, in the male, the most important parts of the stridulatory organ: the file (=Cu2) of the left and the mirror and its frame of the right fore wing (text-figs. 4—7). In *Sexava*, however, Cu1 and its fold reach the hind margin of the fore wing considerably more distally, near or beyond the middle of the wing length and do not delimit a sharply defined triangular area (text-figs. 2, 4, 5). As a result, the first cubital area (between Cu1 and Cu2) in *Sexava* is conspicuously wide and

elongate, which is demonstrated also by the large overlap of the flexed wings, and the considerable extension of the hind margin of the flexed wing beyond the median line of the abdomen. It is noted here that these characters are very distinct in the male, but far less so in the female.

The high taxonomic significance of sound produced by Tettigoniids is widely recognized. Nevertheless, the structure of the stridulatory organ has been little used as a character. The present study makes use of some attributes of the male stridulatory organ, which can be easily examined: the file of the left fore wing and the mirror and its frame of the right one. These have been studied in most of the available males. The length, width and shape of the file, the number and spacial arrangement of its teeth and the shape, and especially the frame of the mirror of the opposite wing, are in most species and subspecies slightly variable and specific distinction is sometimes conspicuous. I did not have the opportunity to analyse the characters of the file as extensively as has been done in some Phaneropterine genera (Emsley, et al., 1967, 1969; Ragge, 1969; Huxley, 1970; Emsley, 1970; Moss, et al., 1970). Instead, I give a short description together with figures of the file and the mirror. As to the latter, it appears that the frame of the mirror, especially a vein modified into a fold along the hind margin of the mirror, is important for specific recognition.

Stridulation of the female in the Mecopodinae has been recorded by Karny (1924: 143), but his record refers to *Macrolyristes*, which is a member of the tribe



Figs. 4—7. Base of left and right male fore wing, dorsal view: 4—5, *Sexava coriacea* (L.); 6—7, *Segestidea novaeguineae* (Brancsik).

Mecopodini. Recently, Lloyd & Gurney (1975: 47—50) reported labral stridulation of a female attributed to *Sexava femorata* (= *Segestidea novaeguineae*). However, the morphological substrate of this kind of stridulation (labrum versus mandibulae) is obscure. A closer study of the fore wings of the female in *Sexavae* reveals that there is a stridulatory apparatus. It consists of rows of minute spines located on the dorsal surface of the veins near the hind margin of the cubito-anal areas of the right fore wing, where the hind margin of the left wing may function as a scraper. Due to uniform appearance throughout the species of the group, no reliable characters were found which would associate females with males of the same species. Similar spines were often found on the male right fore wing, just distally of the mirror.

Characters found to be more or less reliable at species or subspecies level, may be summarized: general appearance; length of fastigium of vertex; shape of pronotal lateral lobe, convexity of pronotal dorsum; fore wing (length, width, shape, archedictyon, apex, male stridulatory apparatus); spines of legs; shape of male subgenital plate and cercus; length of ovipositor; coloration of head, thorax, fore wing and legs.

#### Key to the genera *Sexava*, *Segestes* and *Segestidea*

1. Fore and mid tibiae with a small, posterior, dorso-apical spine (text-fig. 1) (refers to tip of tibia only, not to dorsal margins; if tibia stretched forward, posterior is "lateral" side) . . . . . 2
- These spines lacking (with very few exceptions in *Segestes decoratus*); venation of fore wing as in *Segestidea*, see below . . . . . *Segestes* Stål
2. Cu1 and similarly located fold of fore wing running obliquely toward hind margin of wing at short distance from wing-base, delimiting well-defined triangular area, in male containing the main attributes of the stridulatory organ (text-figs. 3, 6, 7); flexed fore wings, except for triangular area at base, narrowly overlapping each other, hind margin not widely extending over median line of abdomen . . . . . *Segestidea* I. Bolívar
- Cu1 and its fold running to a point of the hind margin of fore wing near or beyond middle of wing-length, without delimiting a well-defined triangular area (text-figs. 2, 4, 5); flexed fore wings overlapping each other widely and over great distance of wing-length, hind margin extending far beyond median line of abdomen over almost whole length . . . . . *Sexava* Walker

#### **Sexava** Walker, 1870

*Sexava* Walker, 1870: 437.

*Moristus* Stål, 1873: 47 (type-species, by monotypy: *Gryllus* (*Tettigonia*) *coriacea* Linné, 1758)

Type-species, by monotypy: *Gryllus* (*Tettigonia*) *lanceolata* Stoll, 1813.

Walker based his genus on a female from Ceram, assigned by him with some doubt to Stoll's *lanceolata*. This species is synonymous with Linné's *coriacea*. Walker's specimen, however, does not agree with *lanceolata* (= *coriacea*), but with Stål's *nubila*, described in 1874, after Walker's publication. Stability and uniformity

of nomenclature is best served when neglecting Walker's misidentification (Article 70 (a) (iii) of the International Code of Zoological Nomenclature). Therefore I propose to maintain the current type-species.

*Sexava*, as indicated by the key above, is a natural group of species, characterized by the presence of posterior dorso-apical spines of fore and mid tibiae (text-fig. 1) in combination with the unusual course of the first cubital vein (Cu1) of the fore wing (text-figs. 2, 4, 5), resulting into the large overlap of the flexed fore wings both with each other and with the median line of the abdomen.

Up till now, the following taxa have been arranged under *Sexava*:

*coriacea* (Linné, 1758) (= *lanceolata* Stoll, 1813)

*nubila* (Stål, 1874) (*Moristus*)

*novaeguineae* (Brancsik, 1897) (*Moristus*)

*karnyi* Leefmans, 1927

*femorata* C. Willemse, 1940

*uniformis* C. Willemse, 1940

*leefmansii* C. Willemse, 1940

*grandis* (C. Willemse, 1955) (*Segestes*)

*rufipalpis* C. Willemse, 1966

Of this list, five taxa apparently belong to *Segestidea*, while only four taxa fit *Sexava* in its present concept: *coriacea*, *nubila*, *karnyi*, and *grandis*. The last will be synonymized with *coriacea* in the present paper.

#### Key to the species of *Sexava*

1. ♂, ♀: smaller, length of fore wing 50—60 mm; lower and part of inner side of proximal half of hind femur solid black; ♂: cercus with short apex (pl. 3 fig. 22), teeth of stridulatory file in posterior half very widely spaced (pl. 4 fig. 28) (Togian Is. and opposite part of Celebes) . . . . . *karnyi* Leefmans
- ♂, ♀: larger, wing-length more than 65 mm; hind femur without black parts; ♂: cercus with apex longer (pl. 3 figs. 18—21); teeth of stridulatory file more closely set (pl. 4 figs. 23—27) . . . . . 2
2. ♂: subgenital plate wider, apical incision shorter, lobes wider, styli shorter (pl. 3 figs. 12—14); cercus with longer, more attenuate apex (pl. 3 figs. 18—19); teeth of stridulatory file narrowly set (pl. 4 figs. 23—25); ♂, ♀: pronotal lateral lobe usually as long as high; apex of flexed wings reaching middle third of hind tibia; ♀: subgenital plate usually shorter than wide; ovipositor longer, 40—50 mm, apex of flexed wings usually not reaching tip of the latter (Sangihe Is.; central Moluccas; ? Celebes; ?? New Guinea) . . . . . *coriacea* (Linné)
- ♂: subgenital plate narrower, apical incision longer, lobes narrower, styli longer (pl. 3 figs. 15—16); cercus with shorter, less attenuate apex (pl. 3 figs. 20—21); teeth of stridulatory file coarser (pl. 4 figs. 26—27); ♂, ♀: pronotal lateral lobe usually narrower, being shorter than high; apex of flexed wings reaching beyond middle of hind tibia, usually apical third; ♀: subgenital plate usually as long as wide; ovipositor shorter, 30—43 mm, apex of flexed wings reaching at least tip of the latter (Northern Celebes; Talaud and Nanusa Is;

southeastern Moluccas; Kei and Aru Is.; western and northeastern New Guinea) . . . . . *nubila* (Stål)

***Sexava coriacea* (Linné, 1758)**

(text-figs. 2, 4, 5, pl. 1 figs. 1—4, pl. 3 figs. 12—14, 18, 19, pl. 4 figs. 23—25, pl. 5 fig. 29, map 1)

*Gryllus* (*Tettigonia*) *coriaceus* Linné, 1758: 430.

*Gryllus* (*Tettigonia*) *lanceolata* Stoll, 1813: 23, pl. 10a figs. 39-40.

*Locusta lanceolata*; de Haan, 1843: 214 (partim).

*Moristius coriaceus*; Stål, 1873: 95.

*Sexava coriacea*; Kirby, 1906: 359.

*Segestes grandis* C. Willemse, 1955: 36, fig. 2. **syn. nov.**

*Sexava grandis*; C. Willemse, 1957: 38 (footnote).

Material studied: Soela Mangoli, Pasi Spah, 18—19.iii.1930, Snellius Exp. (1 ♂ RNH); Ins. Buru, H. Kühn, coll. Br. v. W. (1 ♂ NMW); Batjan, Staudinger, coll. Br. v. W. (1 ♂ NMW); Ternate, 1894, W. Kükenthal (1 ♂ NMW); Halmaheira (1 ♂ 1 ♀ CW), 1894, W. Kükenthal (1 ♀ NMW), Djailolo forêt Todowangi, 16.ii.1929, Prince Léopold (1 ♂ CW); Sangir, A. Reyne, ex coconut palms (1 ♂ 1 ♀ BMNH); Sangir, xi.1948, C. Franssen, coconut leaf, ex coll. S. Leefmans (2 ♀ ITZ); Ambon (1 ♂ CW, 1 ♂ 1 ♀ ITZ), 1863, Hoedt (1 ♀ RNH), 1864, Hoedt (6 ♂ 2 ♀ RNH), Staudinger, coll. Br. v. W. (1 ♂ NMW), 1933, coll. R. Ebner, Rehn don. (1 ♀ NMW), 1859, Doleschal (1 ♀ NMW), 30 m, 1.ix.1961, A. M. R. Wegner, at light (1 ♀ CAS), Waai, 1.viii.1966, A. M. R. Wegner (1 ♀ CAS); Molukken, Depuiset, coll. Br. v. W. (1 ♀ NMW); Java (1 ♂ 1 ♀, De Haan vidit, RNH); Nieuw Guinea (1 ♂ CW); Celebes, 1884, Musschenbroek (2 ♀ ITZ); Obi I. (1 ♀ BMNH).

*Segestes grandis*: type-series, ♂ holotype: Obi Island, Anggai 30.v.1953; ♀ paratype: Obi Island, Laiwui, 20.ix.1953 (both specimens with appropriate identification and type-labels) (CW).

Additional material: Obi (1 ♂ CW), Telaga, 7.viii.1953 (1 ♀ CW), Laiwui, 29.ix.1953 (2 ♂ 1 ♀ CW, 2 ♂ 2 ♀ RNH), Wajaloar — Obi, 27.viii.1953 (1 ♂ RNH) (all identified by C. Willemse).

The Linnean type of *Gryllus* (*Tettigonia*) *coriaceus* could not be traced in London (Ragge & Mrs. Pitkins, in litt. 5.iii.1976).

The possible synonymy of Stoll's *lanceolata* with Linné's *coriacea* is discussed extensively by Karny (1931: 78-82). Stoll's material was from the collection of J. Rajje van Breukelerwaert. This collection was sold 3 July 1827 in Amsterdam and the name *lanceolata* is found under the numbers 372 and 374 (p. 76) of the "Catalogue . . . d'objets d'histoire naturelle . . . Joan Raye de Breukelerwaert . . . sera vendu . . . à Amsterdam . . .". However, the specimens in question could not be traced in the collections at Amsterdam (ITZ) or Leiden (RNH). Nevertheless, the length of the female wings and ovipositor of Stoll's figure 39 makes identification possible. That figure perfectly fits *coriacea* and not *nubila*. Therefore I again propose to synonymize *lanceolata* with *coriacea*.



In the original description, *Segestes grandis* C. Willemse, 1955, was clearly distinguished from other members of that genus. In his 1957 paper, C. Willemse allocated the species correctly to *Sexava*, but distinction among species of that genus was omitted. Comparison of the types and additional topotypes of *grandis* with material of *coriacea* clearly reveals that *grandis* represents merely large individuals which are within the range of variation of *coriacea*. I propose to synonymize both taxa.

*Sexava coriacea* is defined as indicated in the key. A general description can be found under *Segestes grandis* by C. Willemse (1955: 36, fig. 2). Reliable characters are the male subgenital plate (pl. 3 figs. 12—14), cercus (pl. 3 figs. 18—19) and stridulatory file (pl. 4 figs. 23—25). The latter is slightly fusiform and arcuate, 4—8 mm long, number of teeth 48—92, the anterior 25—45 ones almost blunt and covering the anterior fourth, the other teeth sharp and arranged over the remaining length of the file. Width of the file increasing in the anterior third, reaching maximum 0.5—0.9 mm in the middle third, decreasing again posteriorly to about half maximum width. Spacing of teeth narrow, distinctly increasing from the anterior to posterior end of the file, between the posterior teeth about 2—4 times as large as between the anterior sharp teeth. The number of teeth and the maximum width depend mainly on the length of the file, while the spacing of the teeth is quite uniform. The mirror (pl. 5 fig. 29) is about as long as wide, roughly circular with the anterior margin almost straight. Fold of the mirror strongly inflated in the middle, slightly extending over the mirror, its outline from almost straight to slightly sinuate.

Variation. The measurements, especially the length and width of the fore wing (pl. 1 figs. 1—4) vary considerably. While the ovipositor usually extends beyond the apex of the flexed wings, they may be of the same length in the females from Sangihe and Obi Islands (pl. 1 figs. 3—4). The stridulatory file of the studied males from Buru and Ambon (pl. 4 fig. 25) is shorter (4—5.3 mm) and the number of teeth smaller (47—72), while the file in males from other islands (pl. 4 figs. 23, 24) is longer (5.4—8.2 mm) and the number of teeth larger (72—95). The male subgenital plate is variable (pl. 3 figs. 12—14) in width, the margins of the apical incision vary between smooth and slightly serrate and the tips of the lobes from truncate to slightly emarginate. Variation is also observed in the female subgenital plate. As in the stridulatory file, the variation of the subgenital plate of both sexes corresponds with the area of occurrence (compare also Leefmans, 1927b: pl. 5). However, the shape of the male cercus is quite uniform (pl. 3 figs. 18, 19). The pronotal lateral lobe of some specimens is slightly shorter than high. The general colour, usually green, is sometimes brown. Fore wing and hind femur are always of general colour, lacking any pattern.

Measurements: body ♂ 60—85, ♀ 60—71; fore wing ♂ 65—80, ♀ 75—86; hind femur ♂ 43—48, ♀ 45—51; ovipositor 40—50.

Distribution. The range covers the central islands of the Moluccas and the Sangihe Is. The occurrence in Celebes and New Guinea needs confirmation (map 1).

Localities: Ambon (Redtenbacher, 1892: 201; Krauss, 1903: 747; Hebard, 1922: 180; Karny, 1924: 151; Leefmans, 1927b: 13); Buru (Karny, 1926: 183); Batjan

(Karny, 1924: 151); Sula Is. (Karny, 1924: 151), Pasi Spah near Sula Mangole; Obi (Hebard, 1922: 180; Karny in Leefmans, 1927b: 13), Anggai and Laiwui (C. Willemse, 1955: 36), Wajaloar and Telaga; Banggai Is., Labobo (Leefmans, 1927b: 13); Ternate (Brunner v. W., 1898: 199; Leefmans, 1927b: 13); Halmahera, Tobelo (Leefmans, 1927b: 13), Djailolo (C. Willemse, 1933: 9); Sangihe Is. (Leefmans, 1927b: 13); ? Celebes (Karny, 1924: 151).

**Discussion.** The species is well-defined in the male. However, distinction between the female of *coriacea* (pl. 1 figs. 3, 4) and the form of *nubila* (pl. 1 fig. 6), which occurs in the Talaud and Nanusa Is., may be very doubtful. Sometimes the following characters are helpful: the wider thorax, the absence of a series of yellowish dots on the radial area of the fore wing, and the longer ovipositor in *coriacea*.

A relation between the variation described above and the geographic distribution seems unreliable. However, the variation is gradual and no gap of any importance could be found. We are, of course, dealing with isolated populations living in numerous islands, which might explain the observed variation.

Some previous records should be discussed. The one from Ceram appears to be based on Walker's record of *lanceolata* (Walker, 1870: 437). As the specimen is now assigned to *nubila*, the occurrence of *coriacea* in Ceram needs to be confirmed. De Haan's record (1843: 214) of *lanceolata* from "Timor, Java" should be considered unreliable as it was done by Karny (1931: 83). De Haan's material examined consists of 2♂ 2♀ (RNH), all labelled "Java". One pair agrees with *coriacea* (as from Ambon), the other pair with *nubila* (as from the Moluccas). The occurrence of *coriacea* in Celebes should be confirmed, as it was based on 2♀ of doubtful origin before me and another ♀ recorded by Karny (1924: 151). The same can be said of its occurrence in New Guinea, which is based on 1♂ 3♀ from Hollandia (Karny, 1924: 151) and 1♂ at hand of doubtful origin, labelled "Nieuw Guinea". All Hollandia and other material from New Guinea before me belongs to *nubila*.

### ***Sexava nubila* (Stål, 1874)**

(pl. 1 figs. 5, 6, pl. 2 figs. 7—9, pl. 3 figs. 15, 16, 20, 21, pl. 4 figs. 26, 27, map 1)

*Moristus nubilus* Stål, 1874: 96.

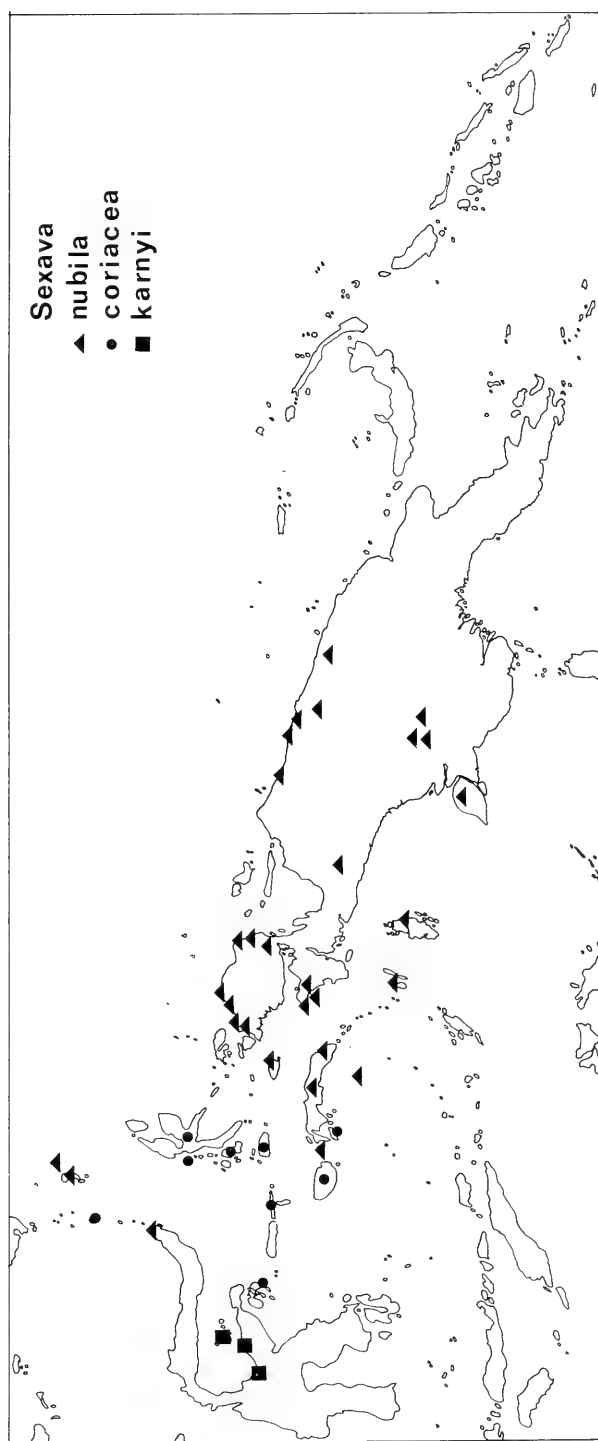
*Sexava lanceolata* (nec Stoll); Walker, 1870: 437.

*Locusta lanceolata*; De Haan, 1843: 214 (partim).

*Sexava nubila*; Kirby, 1906: 359.

**Material studied:** ♀ holotype, labelled: 292 76 (NR) (parts of antennae lacking, apex of fore wings slightly damaged).

**Additional material:** Celebes, Manado, i.1932, A. Reyne (1♂ BMNH); Talaud Is., A. Reyne, ex coconut palms (1♂ 1♀ BMNH), iv.1949, C. Franssen, on coconut, ex coll. S. Leefmans (1♂ 1♀ ITZ), Beo, 14—21.vi.1930, Snellius Exp. (6♂ 3♀ RNH); Manipa, 1864, Hoedt (1♂ RNH); Ceram (1♀ BMNH), Rukuwa, 30 km E. of Amakar Kowsuto, 3.v.1970, R. F. Ellen (1♂ 1♀ BMNH); Misool, 1870 (1♀ ITZ); Kei Is., C. Ribbe, coll. Br. v. W. (1♂ NMW), Kühn, coll. Br. v. W. (1♀



Map 1. Distribution of *Sexava* species.

NMW), 1903 (1♂ BMNH); Aru-Inseln, C. Ribbe, coll. Br. v. W. (1♂ 1♀ NMW); Banda Is., 5° S, 130° E, 6.iv.1975, J. E. Lloyd (1♂ CW); West New Guinea: Sekroë, iii.1897, Schaedler (3♂ RNH); Fak Fak, viii.1874, C. J. L. Palmer (4♂ 3♀ RNH); Poel Pandjang or Noha, viii.1904, Jhr. v. Nanhuijs (1♀ RNH); Sorong, 1.iii.1929 (1♂ 2♀ CW) & entre Sakoemi et Moemi, 13.iii.1929 (1♀ CW) & Manoi — Salawati, 2.iii.1929 (2♂ CW), Prince Léopold; Sedorfojo, vii.1952 (1♂ RNH) & Seribaai, 5.viii.1952 (1♂ RNH), Mevr. Marcus v. d. Nieuwenhuizen; Komara, ii.1963, Hr. & Mevr. Marcus v. d. Nieuwenhuizen (1♂ RNH); Jef Lie, 18.ii.1957 (3♂ 2♀ CW) & Sansapor, vi.1961 (1♂ 1♀ CW) & Mega, 22.vii.1961 (1♂ CW) & Koor, 26.vii.1961 (1♂ CW), R. T. Simon Thomas; Andai, acq. 1870, Rosenberg (1♀ RNH); Paniai, 27.xi.1939, Nieuw Guinea Exp. N.A.G. 1939 (1♂ RNH); Bernhard camp, 50 m, vii.1938, J. Olthof, Neth. Ind. Amer. New Guinea Exp. (1♂ 1♀ RNH); Maffin Bay, vi.1944, E. S. Ross (1♂ 3♀ CAS); Hollandia, 1955—1956, A. Klaassen (1♀ RNH), Ned. Nw. Guinea Exp. 1911, Dr. P. N. v. Kampen (3♂ 6♀ RNH), vii.1938, L. J. Toxopeus, Neth. Ind. Amer. New Guinea Exp. (1♂ RNH); Zoutbron, vi—vii.1911, Ned. Nw Guinea Exp. 1911, Dr. P. N. v. Kampen (1♀ RNH); Tanah Merah baai (South New Guinea), 19.viii.1910, Ned. Nw Guinea Exp. 1911, Dr. P. N. v. Kampen (1♂ RNH); Mindiptana, 26.xi.1958, Br. Monulphus (1♂ CW, 1♀ RNH); Mariang a. d. Digoel, 10 m, 12.ix.1959 (1♂ RNH) & Kouh a. d. Digoel, 8.ix.1959, 10 m (8♂ 7♀ RNH) & Kowage, 10 m, 8.ix.1959 (6♂ 1♀ RNH) & Hijob, 25 m, 10.ix.1959 (1♂ 2♀ RNH), Neth. New Guinea Exp. Star Range; Java (De Haan vidit) (1♂ 1♀ RNH); Sepik District (East New Guinea), Bainyik, 1.xii.1959 & 11.xii.1953, J. H. Ardley (2♀ DASF).

Stål described the species after a female. Sjöstedt (1933: 14, pl. 25 fig. 1), however, figured a male as Stål's type. Dr. T. Kronstedt (in litt. 24.iii.1976) informed me as follows:

"1. The specimen which Sjöstedt figured is the only one placed under the label *Sexava nubila* in our collection, and it is obviously the same specimen as he figured.

2. The same drawer contains also 3 specimens placed under *coriacea* L., two of which bear a name label "*coriacea*", one without any label. . . . Assuming that the one lacking any label is the type of *nubila*, we compared the measurements given in Stål's original description with the measurements given in his redescription of *coriaceus*. It then turned out that Stål's measurements given for *coriaceus* fitted the specimen which he had labelled as such and his measurements given for *nubila* fitted the specimen without labels.

3. The male specimen labelled *nubilus* bears labels in Stål's handwriting "*Moristus Stal*" and "*nubilus Stal*" as well as a label "*Platyphyllum coriaceum* (?) L. Serv." and a red printed label "*Typus*", the latter apparently put on by Sjöstedt."

Presumably, when Sjöstedt figured the type of Stål's *nubilus*, the male erroneously beared Stål's labels instead the female. The latter specimen is before me and agrees fully with Stål's description. It is considered the holotype of *Moristus nubilus* (pl. 2 fig. 7).

The additional material at hand from New Guinea, Kei and Aru Is. and the southeastern Moluccas agrees with the holotype. The particular form of the

species occurring in Talaud and Nanusa Is. is discussed below.

The species is defined as indicated in the key. Quite characteristic are the shape of the male subgenital plate (pl. 3 figs. 15, 16), the cercus (pl. 3 figs. 20, 21) and the stridulatory file (pl. 4 figs. 26, 27). The latter, compared with *coriacea*, is less fusiform and arcuate, 5.5.-7.0 mm long, number of teeth 54-65 of which the anterior 10-20 are fine and about blunt, covering the anterior sixth to eighth part of the file. Width of the file strongly increasing in the anterior part, reaching maximum 0.6-0.8 mm in the middle third, decreasing posteriorly but slightly. Spacing of the teeth wider than in *coriacea*, moderately increasing posteriorly, distance between successive posterior teeth 1-2 times as large as between the anterior sharp teeth. Mirror and its frame of the right male fore wing slightly different from that in *coriacea*, but the available material of the latter does not allow reliable conclusions.

Variation. In spite of individual variation, the shapes of the male subgenital plate, cercus and stridulatory file, are rather uniform throughout the material at hand, including that from Talaud Is. The same can be said of the female subgenital plate, figured by Leefmans (1927b: pl. 5 fig. 3). Material from New Guinea (pl. 1 fig. 5, pl. 2 fig. 8), Kei and Aru Is. and the southeastern Moluccas is uniform in general appearance (slender) and coloration (brown). However, that from Talaud Is. (pl. 1 fig. 6, pl. 2 fig. 9), Nanusa Is. (cf. Leefmans, 1927b and the male from northern Celebes differ in more robust general appearance, wider thorax, wider and comparatively shorter wings and often green general colour. The lower sides of the femora of a male from Banda are dark brown, but not solid black. In all material at hand, usually a series of distinct dark brown flecks with a central yellow dot on the radial area of the fore wing is present.

Measurements: body ♂ 55-72, ♀ 50-70; fore wing ♂ 68-80, ♀ 75-86; hind femur ♂ 35-43, ♀ 38-43; ovipositor 30-43.

Distribution (map 1). The range covers northeastern and all western New Guinea, Kei and Aru Is., southeastern Moluccas, extending into the Talaud and Nanusa Is. and (?) northern Celebes.

Localities: Celebes: Manado; Talaud and Nanusa Is. (Leefmans, 1927b: 13; Oudemans, 1927: 267; Franssen, 1954: 99-102; Reyne, 1960: 232); Manipa (between Buru and Ceram); Ceram (Walker, 1870: 437), East Central and Watai (Karny, 1924: 151), Rukuwa; Banda; Misool; Kei Is. (Redtenbacher, 1892: 201; Karny, 1926: 183); Aru Is. (Redtenbacher, 1892: 201); West New Guinea: Sekroë; Pandjang I.; Sorong (C. Willemse, 1933: 9); Sakoemi-Moemi; Manoi-Salawati (C. Willemse, 1933: 9); Sedorfojo; Seribaai; Komara; Jef Lie; Sansapor; Fak Fak; Mega; Koor; Andai; Manokwari (C. Willemse, 1933: 9); Paniai; Bernhard Camp; Maffin Bay; Hollandia (Karny, 1924: 151); Zoutbron; South New Guinea; Tanah Merah baai; Süd-Neuguinea (Karny, 1924: 151); Frederik-Hendrik I. (Karny, 1924: 151); Mindiptana; Mariang; Kouh; Kowage; Hijob. East New Guinea: Sepik distr., Bainyik.

Discussion. The species is well-defined in the male. The female of the form occurring in the Talaud and Nanusa Is., however, resembles strongly that of *coriacea*. Their distinction is discussed above under the latter species. Besides, the

female of *nubila* resembles superficially that of *Segestidea novaeguineae*. The latter differs in more oblique course of Cu1 of the fore wing, stronger ventral spines of the hind femur and in colour pattern of the hind leg.

A record of *nubila* from Java (K. K. Hofmuseum Wien) by Redtenbacher (1892: 201) is unreliable (Karny, 1924: 151). His material could not be traced in the Vienna museum (Kaltenbach, in litt. 12.xi.1975). The pair labelled "Java" of De Haan is discussed under *coriacea*, and the locality is considered unreliable. Karny's record (1924: 151) from Batjan was based on 1 ♀ while 1 ♂ 2 ♀ of the same series (originating from Leefmans) were assigned to *coriacea*. I doubt the correct identification of the "*nubila*" female. The occurrence of *nubila* in Batjan should be confirmed, based on a male. Of zoogeographic interest is the Manado male (N. Celebes), which agrees fully with the *nubila* form of the Talaud and Nanusa Is. This single record needs confirmation as the locality appears isolated from the known range of the species (map 1).

### ***Sexava karnyi* Leefmans, 1927**

(pl. 2 figs. 10, 11, pl. 3 figs. 17, 22, pl. 4 fig. 28, map 1)

*Sexava karnyi* Leefmans, 1927a: 411, figs. 1-5 (type-locality: Poat I.).

Material studied: Kp. Baroe (Ampana M. Cel.), viii.1949, A. Cohen, on coconut (1 ♂); Posso, ix.1948, Dr. C. Franssen, on coconut leaf (1 ♀) (both ex coll. Dr. S. Leefmans, ITZ).

The types of this species could not be traced. The material before me (pl. 2 figs. 10, 11) agrees completely with the description and figures of *karnyi*. The fore wing, which is wide and rather tapering apically, shows the venation characteristic in *Sexava*.

The species is defined in the key. The stridulatory file (pl. 4 fig. 28) of the available male is 6.5 mm long, number of teeth 60, of which the anterior 35 about blunt and covering the anterior fourth of the file length. Width of the file increasing in anterior half, reaching a maximum of 0.4 mm in middle, decreasing posteriorly to 0.2. mm. Spacing of the teeth conspicuously increasing posteriorly, greatest distance between successive posterior teeth about 10 times more than between the anterior sharp teeth. Mirror and its frame of right male fore wing much as in the other two species of the genus. Flexed wings reach the apical third of hind tibia and tip of ovipositor. The male subgenital plate (pl. 3 fig. 17; Leefmans, 1927a: fig. 2) resembles much that in *nubila*. The male cercus (pl. 3 fig. 22) has a robust and short apex, bearing a minute spine on its anterior edge. The female subgenital plate of the available specimen appears more widely emarginate than in the figure by Leefmans (1927a: fig. 3). The coloration of the pair agrees fully with the original description: general colour brown, lower and inner side of proximal part of hind femur conspicuously solid black.

Measurements (partly after Leefmans): body ♂ 53—58, ♀ 48—54; fore wing ♂ 52—53, ♀ 56—60; hind femur ♂ 36—40, ♀ 38—39; ovipositor 26—27.

Distribution. Known only from Togian Is. and the southern opposite part of Celebes (map 1).

Localities: Poat I. (Leefmans, 1927a: 412); Celebes: Posso; Ampana.

Discussion. The species is well-defined, especially by the male stridulatory file and the coloration of the hind femora. Variation is insufficiently known. Previously recorded only from the type-locality.

***Segestes* Stål, 1877**

*Segestes* Stål, 1877: 45; Redtenbacher, 1892: 189, 197.

Type-species by monotypy: *Segestes vittaticeps* Stål, 1877.

*Segestes* is characterized, as noted in the key, by lacking the dorso-apical spines of fore and mid tibiae in combination with usual course of Cu1 of the fore wing, delimiting a well-defined triangular area which, in the male, contains the main attributes of the stridulatory apparatus. As pointed out above under the generic characters, exceptionally a dorso-apical spine has been found on the fore and mid tibiae of some specimens considered *Segestes decoratus*.

Up to now, the following taxa have been arranged under *Segestes*:

*vittaticeps* Stål, 1877

*punctipes* Redtenbacher, 1892

*unicolor* Redtenbacher, 1892

*fuscus* Redtenbacher, 1892

*decoratus* Redtenbacher, 1892

*frater* Hebard, 1922

sp. Leefmans, 1927

*celebensis* Karny, 1931

*beieri* Kästner, 1934

*acuminatus* Kästner, 1934

*grandis* C. Willemse, 1955 (correctly assigned to *Sexava* by C. Willemse, 1957)

The latter taxon is synonymized with *Sexava coriacea* (see above) and *acuminatus* is now transferred to *Segestidea*. Of the other species three occur in the Philippines, one in Palau I., one in Celebes, one in Obi and one in New Guinea. The typespecies, *unicolor* from Palau I. and *decoratus* from New Guinea, will be discussed, while the other species are shortly memorized only. Three new species from New Guinea will also be described. Provisional keys to previously recognized species were given by Redtenbacher (1892: 198), Kästner (1934: 46), and C. Willemse (1961: 107). When using these keys, it is noted here that styli of the male subgenital plate of *vittaticeps* were incorrectly thought to be lacking. A key to the species occurring in New Guinea is given below.

***Segestes vittaticeps* Stål, 1877**

(pl. 6 fig. 30, pl. 7 fig. 34, pl. 9 figs. 48, 53, pl. 10 fig. 64)

*Segestes vittaticeps* Stål, 1877: 45.

The species is known from the syntypes (1 ♂ 1 ♀ RN), 1 ♂ (NMW) recorded by

Redtenbacher (1892: 198) (misidentification?) and 1 ♂ 2 ♀ (ANSP) recorded by Hebard (1922: 176). The syntypes were figured by Sjöstedt (1933: 14, pl. 22 figs. 2, 3) and the male subgenital plate of Redtenbacher's male by Kästner (1934: 47, fig. 14).

The male syntype is before me and hereby designated lectotype (pl. 6 fig. 30, pl. 7 fig. 34). It is labelled: Ins. Philipp., Semper, *Segestes vittaceps* Stål, Typus. The specimen agrees with Stål's description and Sjöstedt's figure, but lacks part of the stridulatory file, which was not so in Sjöstedt's figure, and the position of the legs differs also slightly from that figure.

#### Redescription.

Small (pl. 6 fig. 30, pl. 7 fig. 34). Fastigium of vertex obtusely pointed, reaching about middle of scape, shallowly sulcate. Pronotum with dorsum somewhat flattened medially, slightly rounded laterally, anterior margin slightly convex, posterior margin straight; lateral lobe slightly longer than high, deepest point of lower margin about in the middle, from there rounded, posteriorly more so than anteriorly.

Flexed wings extending just behind hind knee. Fore wing narrow, in distal half gradually tapering toward narrowly rounded apex; archedictyon well developed, membrane more or less opaque; Cu1 running obliquely toward hind margin of wing, almost reaching the latter at short distance from wing-base and from there parallel and close to hind margin of wing, vanishing into archedictyon about middle of wing length; stridulatory area well-defined, file partly lacking; mirror (pl. 10 fig. 64) twice as long as wide, elongate-elliptical, fold extending slightly over mirror, its outline almost straight and parallel to anterior margin of mirror.

Fore and mid femora unarmed. All knee-lobes with one spine. Fore tibia without dorsal spines, mid tibia with 2 dorsal spines on distal half of posterior margin, no dorso-apical spines. Apical half of hind femur with series of ventral spines.

Cercus (pl. 9 fig. 53) almost rectangularly incurved in apical fourth, gradually tapering to a short tooth. Subgenital plate (pl. 9 fig. 48) strongly elongate, slightly narrowing apically, apex divided by comparatively deep, narrowly parabolic incision into pair of lobes, tips of the latter truncate with distinct styli.

General colour pale brown ("olivaceo-virescens" in Stål's description). Median black stripe over occiput, narrowing anteriorly and reaching fastigium of vertex. Hind margin of fore wing narrowly yellowish-white. Lower and inner sides of proximal half of hind femur solid black. Spines of legs with tips black, of hind femur black at their bases.

Measurements: body 39; fore wing 33; hind femur 28.

Distribution. As far as now only known from the Philippine Is.: — (Stål, 1877: 45; Redtenbacher, 1892: 198); Surigao, Mindanao (Hebard, 1922: 176).

Discussion. Redtenbacher and Kästner based their diagnosis of *vittaceps* on a male in the Vienna museum. The subgenital plate of this specimen, figured by Kästner, lacks the styli, a character used in their keys to the species. Whether this difference with Stål's type is of much importance is an open question.



**Segestes punctipes** Redtenbacher, 1892

*Segestes punctipes* Redtenbacher, 1892: 199.

Known only from the ♀ holotype (NMW). The species is discussed by Hebard (1922: 177).

Distribution. Philippine Is., without precise locality.

**Segestes fuscus** Redtenbacher, 1892

*Segestes fuscus* Redtenbacher, 1892: 199.

Known only from the ♀ holotype (NMW).

Distribution. Philippine Is., without precise locality.

**Segestes celebensis** Karny, 1931

*Segestes celebensis* Karny, 1931: 72, fig. 37.

Known only from the ♂ holotype and 1 juvenile ♀ (depository?).

Distribution. Celebes: Matinang-Kette & Minahassa, Karowa-Popo.

**Segestes beieri** Kästner, 1934

*Segestes beieri* Kästner, 1934: 48, figs. 15—17.

Known only from the syntypes (1 ♂ 1 ♀ NS).

Distribution. Philippine Is.: Mindoro (Kästner, 1934).

**Segestes frater** Hebard, 1922

*Segestes frater* Hebard, 1922: 177, pl. 16 fig. 2.

Known only from the ♀ holotype (ANSP) and 1 ♂ (NS). The latter was described by Kästner (1934: 51, figs. 20, 21). I have before me a female from Laiwui, Obi, 29.ix.1953 (CW), which agrees with Hebard's description except for the coloration, which is unicolorous green.

Distribution. Known only from the Moluccas: Obi (Hebard, 1922: 177; Kästner, 1934: 51).

**Segestes** sp. Leefmans, 1927

*Segestes* sp. Leefmans, 1927b: 15, pl. 5 fig. 4, pl. 6 fig. 4.

According to Leefmans (1927b) and Karny's opinion, a not yet described species from Loleba I., near Halmaheira. I could trace only one discoloured female in bad condition, labelled: *Segestes* spec. Loleba I. (Halmaheira) sent by Leefmans (BNNH). The specimen agrees with Leefmans' data but by lack of the male, further comments are postponed.

**Segestes unicolor** Redtenbacher, 1892

(pl. 6 fig. 32, pl. 7 fig. 35, pl. 9 fig. 54, pl. 10 fig. 59)

*Segestes unicolor* Redtenbacher, 1892: 199.

Known from the ♀ holotype (NMW) and another ♀ (BPBM) recorded by C. Willemse (1951: 342). I have before me 2♂ labelled: West Caroline Is., Koror, Palau, 1.xii. & 20.x.1971, M. R. Lundgren (CAS). Presumably, on the basis of topographic evidence, these males represent *unicolor*.

## Description of male.

Small (pl. 6 fig. 32, pl. 7 fig. 35). Head, thorax and wings as in *vittaticeps*. Stridulatory file (pl. 10 fig. 59) slightly arcuate and fusiform, 2.9—3.0 mm long, number of teeth 100—110, of which anterior 20—30 ones fine, blunt and covering anterior sixth of file length. Width of file reaching maximum 0.2 mm at the end of proximal fourth of file length, decreasing slightly posteriorly. Spacing of teeth almost regular. Stridulatory area of right fore wing as in *vittaticeps*.

Anteroventral margin of fore and mid femora with 1—3 spines in apical half. Knee-lobes with one spine. Fore tibia without dorsal spines, posterodorsal margin of mid tibia with 5 spines, no dorsoapical spine. Hind femur with series of ventral spines.

Cercus (pl. 9 fig. 54) slender, incurved in apical fourth, rather abruptly tapering to short, slightly incurved apical tooth. Subgenital plate as in *vittaticeps*.

Unicolorous pale brown or pale green, except for yellowish-white hind margin of fore wing and spines of legs, which are completely black or with tips black.

Measurements: body 36—37; fore wing 38—39; hind femur 27—28.

Distribution. Known only from Pelew (Redtenbacher, 1892) or Palau I. (C. Willemse, 1951), West Caroline Is.

Discussion. As far as can be judged now, the species differs from the type-species mainly in the shape of the male cercus and the uniform coloration. A record under the name *unicolor* by Karny (1924: 150) from Neu-Pommern (= New Britain) probably does not refer to this species, but to *Segestes decoratus*.

Among the material before me from New Guinea and the Bismarck Archipelago, four species of *Segestes* can be recognized: *decoratus* Redtenbacher, *cornelii* sp.n., *stibicki* sp.n., and *brevipennis* sp.n.

Key to the species of *Segestes* from New Guinea and the Bismarck Archipelago

1. Fastigium of vertex (pl. 9 figs. 46, 47) long, reaching at least apical margin of scape, apex acute, thorn-like; apex of fore wing wide, more or less truncately rounded; knee-lobes usually with one spine; ♂ subgenital plate with or without styli . . . . . 2
- Fastigium of vertex (pl. 9 fig. 45) shorter, by far not reaching apical margin of scape, apex obtusely pointed; apex of fore wing narrowly rounded; knee-lobes usually with two spines; ♂ subgenital plate with styli, cercus, stridulatory file

- and mirror with frame as in pl. 9 figs. 49, 55, pl. 10 figs. 60, 65 (NW and E. New Guinea, western New Britain) . . . . . *decoratus* Redtenbacher
2. Larger, wing length ♂ ♀ 57—64 mm (pl. 6 fig. 31, pl. 7 fig. 40); ♂ subgenital plate without distinct styli, cercus, stridulatory file and mirror with frame as in pl. 9 figs. 50, 56, pl. 10 figs. 61, 66 (East New Guinea) . . . . . *cornellii* sp.n.
- Smaller, wing-length ♂ ♀ 32-47 mm (pl. 7 figs. 38, 39, 41, pl. 8 figs. 42—44); ♂ subgenital plate with styli as in pl. 9 figs. 51, 52 . . . . . 3
3. Fastigium of vertex reaching 2nd—3rd antennal segment (pl. 9 fig. 47); ♂ subgenital plate with narrow, parallel-sided apical incision and distinct styli (pl. 9 fig. 51); ♂ stridulatory file about 2.4 mm long with about 150 teeth (pl. 10 fig. 62) (East New Guinea: Madang District) . . . . . *stibicki* sp.n.
- Fastigium of vertex shorter, reaching apical margin of scape; ♂ subgenital plate with V-shaped apical incision and minute styli (pl. 9 fig. 52); ♂ stridulatory file about 2 mm long with about 71 teeth (pl. 10 fig. 63) (West New Guinea) . . . . . *brevipennis* sp.n.

### ***Segestes decoratus* Redtenbacher, 1892**

(pl. 6 fig. 33, pl. 7 figs. 36, 37, pl. 9 figs. 45, 49, 55, pl. 10 figs. 60, 65, map 2)

*Segestes decoratus* Redtenbacher, 1892: 18, fig. 4; Kästner, 1934: 52.

*Segestes unicolor*; Karny, 1924: 150(?).

*Eumossula gracilis*; C. Willemse, 1958: 122 (only Buvia); F. Willemse, 1966: 48 (same).

*Segestidea insulana*; F. Willemse, 1966: 48 (only Buvia).

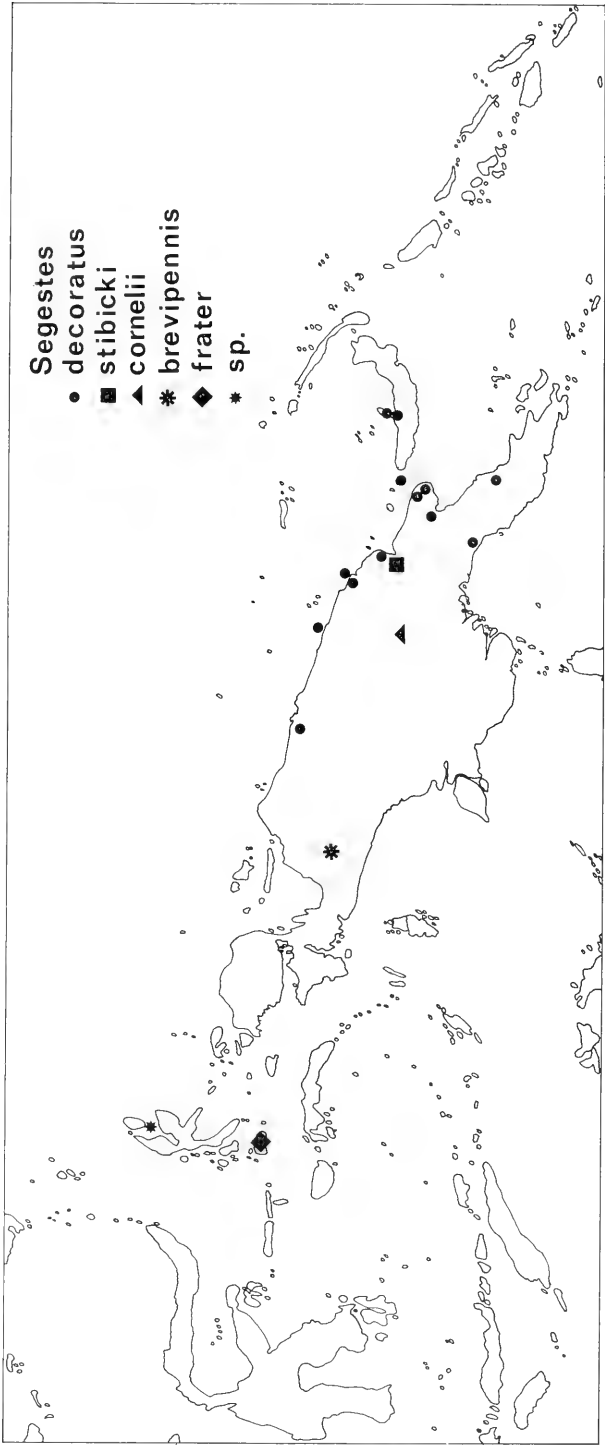
*Sexava femorata*; F. Willemse, 1966: 49 (only 1 ♀ Manam I.).

*Sexava* species B: O'Connor, 1959: 122.

This species was badly known. It was described after a pair from "Neu-Guinea". The male could not be traced in the Vienna museum (Kaltenbach, in litt. 11.ii.1976). The female is before me and is considered holotype (pl. 7 fig. 36). Kästner (1934) recorded additional material from "Neu-Guinea", but gave no further comments. The material listed below agrees with the holotype.

Material studied: ♀ holotype, labelled: Coll. Br. v. W. Neu-Guinea Fruhstorfer, det. Br. v. W. *Segestes decoratus* Redt., Typus, 18 366 (NMW) (lacks parts of tarsi; left side of head and thorax slightly crushed).

Additional material: N. Nov. Guinea, Boven Sermowai, NNW 400 m, 1—8.vi.1911, N.K.G. (= NW New Guinea) (1 ♂ RNH); Gulf District, Murua Agric. Stat. near Kerema, vii.1959, F. X. Rayan, on cocos (1 ♂ 1 ♀ DASF); Northern District, Popondetta, Casey's Plantation, xi.1960 & 10.v.1960, G. S. Dunn, under the bark of bush trees (1 ♂ 1 ♀ DASF); Morobe District, Siassi I., 6.xii.1969, A. Hinton, defoliating coconut palms (1 ♂ DASF); Agric. Exp. Stat. Buvia near Lae, 28.iii.1955, J. Szent-Ivany, on coconut frond (1 ♂ *Segestidea insulana* det. C. Willemse 1958 & 1 ♂ 1 ♀ *Eumossula gracilis* det. C. Willemse 1958, CW); Buvia Agric. Stat., 20.iii.1957, Luna de Carvalho (1 ♀ BMNH); Buvia via Lae, 12.vii.1960, A. Catley, feeding on *Cocos nucifera* (5 ♂ 5 ♀ CW); Deutsch Neu-Guinea, Sattelberg, H. Rolle, Berlin (1 ♂ CW); Siki via Finschhafen, 20.vii.1960, A. Catley, ex *Cocos nucifera* (1 ♂ DASF); Madang District, Manam I., Baliau



Map 2. Distribution of *Segestes* species.

Village, 26.ix.1960, J. I. Cox (1 ♀ *Sexava femorata* det. C. Willemse, CW); Awar Plantation, via Bogia, xi.1960, J. I. Cox (3 ♂ 2 ♀ CW); Madang, 4.v.1932, J. L. F., coconuts (1 ♂ BMNH); West New Britain, Bitokara C. M., Talasea, 26.ii.1971, T. Laklo, on coconuts (5 ♀ DASF); Talasea, Volupai Plantation, 10.v.1966, D. F. O'Sullivan (1 ♀ DASF); West New Britain, Lingalinga Plantation, vi.1959, J. H. Barrett, on *Theobroma* (1 ♀ DASF); West New Britain, Wakanaka Village, 23.i.1974, C. H. Perry, resting in fronds of coconut (1 ♀ DASF).

### Redescription.

♂ (pl. 6 fig. 33), large. Fastigium of vertex (pl. 9 fig. 45) extending but slightly beyond antennal scrobae, reaching middle of scape or shorter, apex obtusely pointed, often with shallow furrow. Pronotal dorsum strongly rounded laterally, anterior margin slightly convex, posterior one straight. Lower margin of pronotal lateral lobe obtuse-angulately rounded, deepest point just distally of middle of lobe length, from there slanting upwards, posteriorly steeper than anteriorly.

Flexed wings reaching middle of hind tibia or slightly shorter. Fore wing narrow, tapering gradually towards narrowly rounded apex; moderate archdictyon. Stridulatory file (pl. 10 fig. 60) scarcely arcuate, 3.5–4.0 mm long, number of teeth 183–196, of which anterior 50–60 fine, more or less blunt and covering anterior fifth to sixth of file length, the other 130–140 ones sharp. Width of file reaching maximum 0.4–0.5 mm at end of proximal fourth of file length, decreasing posteriorly to one-third of maximum width. Spacing of teeth slightly increasing posteriorly, comparatively more in anterior than in posterior part of file. Mirror (pl. 10 fig. 65) about twice as long as wide, roughly elliptical with antero-apical margin angulate; fold moderately extending over mirror, outline sinuate.

Fore femur with 0–3, mid femur with 0–1 spines on anteroventral margin. All knee-lobes with a larger dorsal and a smaller ventral spine; occasionally hind knee-lobe with three and fore knee-lobe with one spine. Fore tibia with 0–1, mid tibia with 5–8 dorsal spines on posterior margin; dorso-apical spines usually lacking.

Cercus (pl. 9 fig. 55) incurved, tapering apically to short and distinctly incurved tooth. Subgenital plate (pl. 9 fig. 49) almost four times as long as smallest width, lateral margin slightly concave in the middle; apex divided by arrowly parabolic incision into pair of lobes with obliquely truncate or slightly sinuate tips. Stylus comparatively long, inserted in lateral half of tip of lobe and usually pointing inward.

General colour green or, less often, brown. Antennae unicolorous or very slightly annulated pale and dark. Palpi from orange via yellowish to pale brown. Head and pronotum unicolorous, but usually with pale orange-yellow stripe running from behind eye toward antero-ventral angle of pronotum, extending over lower margin of pronotal lateral lobe and similarly coloured median stripe from occiput over pronotal dorsum. Lateral stripes may extend over pleurae and median one over cubito-anal areas of fore wing. Fore wings of general colour, immaculate, membrane ranging from little transparent to slightly opaque. Legs of general colour or yellowish, lower and partly inner side of hind femur orange in

green specimens, reddish brown in brown specimens. Knees either of general colour or black from below, or sometimes completely black. Spines of legs with tips black or black basally. Tibiae and tarsi of general colour, tarsi dull brown from below or sometimes completely dark brown.

♀ (pl. 7 figs. 36, 37), larger than male. Wings comparatively long, as in male. Ovipositor with upper margin straight, reaching middle of hind tibia, in dorsal view covered by flexed wings or almost so. Subgenital plate wide, triangular, with median apical emargination. Coloration as in male, basal part of hind margin of fore wing often narrowly orange or yellow.

Variation. It is of particular interest to note that in some specimens the left or right fore and mid tibiae have a posterior dorso-apical spine. This was found in three out of seven females, all from New Britain. Otherwise the specimens agree fully with the material from New Guinea. Whether the instability of this generic character is limited to the population of New Britain is an open question. It is advisable to study the associated males from New Britain to establish the conspecificity with *decoratus*.

Measurements: body ♂ 51—54, ♀ 56—61; fore wing ♂ 52—59, ♀ 63—72; hind femur ♂ 32—37, ♀ 39—42; ovipositor 32—35.

Distribution. The range covers the eastern half of the mainland of New Guinea, extending into some islands near its coast and New Britain (map 2).

Localities: Neu-Guinea (Redtenbacher, 1892; Kästner, 1934); West New Guinea: Sermowai near Hollandia; East New Guinea, East Sepik District: Mushu I. (O'Connor, 1959); Madang District: Madang; Awar Plantation near Bogia (O'Connor, 1959); Baliau Village, Manam I.; Gulf District: Murua Agric. Stat. near Kerema; Northern District: Casey's Plantation near Popondetta; Morobe District: Siki near Finschhafen; Bubia near Lae and Agric. Stat. Bubia; Sattelberg; Siassi I.; West New Britain District: Bitokara C. M. near Talasea; Volupai Plantation near Talasea; Wakanaka Village; Lingalinga Plantation.

Discussion. The species is well-defined and easily distinguished from other *Segestes* species. However, *decoratus* may resemble some species of *Segestidea*, especially *uniformis* (C. Willemse) and *gracilis* (C. Willemse). As noted above, in some specimens of *decoratus* from New Britain dorso-apical spines of fore and mid tibiae are present, which is misleading as to correct generic assignment. In these cases, the following notes may be helpful.

*Segestidea uniformis* (C. Willemse), which occurs in the Admiralty Is. (Manus District), has the pronotal lateral lobe narrower, its lower margin not yellow but of similar colour as the lobe and the deepest point not beyond but about midway the length. The male subgenital plate (pl. 15 fig. 93) is narrower and the male cercus (pl. 15 fig. 101) shorter. The male stridulatory file is about similar but the number of teeth is smaller (130—140 versus 183—196) and the spacing of the teeth more widely (pl. 16 fig. 109); the mirror is distinctly less covered by the fold (pl. 18 fig. 117). Head, thorax, wings and legs are unicolorous.

*Segestidea gracilis* (C. Willemse), both in the nominate subspecies (known from New Ireland District) and in *simulatrix* ssp.n. (known from New Britain), has the wings shorter and the ovipositor longer (pl. 12 figs. 77—79, pl. 13 figs. 80—82). The

lower margin of the pronotal lateral lobe is not yellow but of general colour, slightly convex and not at all obtuse-angulately rounded. The male subgenital plate and cercus are smaller (pl. 15 figs. 94, 95, 102, 103). The male stridulatory file in *simulatrix* is of similar shape, but the number of teeth is much smaller (117–139 versus 183–196) and their spacing much wider (pl. 16 fig. 111), while the shape of the file in nominate *gracilis* is quite distinct, its anterior half being much narrower (pl. 16 fig. 110). Head, thorax, legs and wings are unicolorous.

Karny (1931: 72), who had the species not before him, doubted as to the correct arrangement of *decoratus* under *Segestes*, based on the number of spines of the knee-lobes and the presence of styli of the male subgenital plate. The material at hand demonstrates clearly the variability of the number of spines, and the styli are present in the type-species of *Segestes*. Karny's presumption may be, however, of some importance, but for other reasons, viz., the occasional presence of the fore and mid tibial dorso-apical spines. Material recorded under *Sexava* species B by O'Connor (1959) was not available, but certainly refers to *decoratus*. Karny's record of *Segestes unicolor* Redtenbacher from Neu-Pommern (= New Britain) may refer to *decoratus* rather than *unicolor*, which is known only from the West Caroline Island Palau. I have not examined his material.

### ***Segestes stibicki* spec. nov.**

(pl. 7 figs. 38, 41, pl. 8 figs. 42, 43, pl. 9 figs. 47, 51, 57, pl. 10 figs. 62, 67, map 2)

The species is named after Dr. J. L. Stibick, whose activities urged me to this study.

Material studied: ♂ holo-, 8 ♀ paratypes, labelled: Madang District, Kaironk area, xii.1971-i.1972, J. Menzies (♂ holo-, 6 ♀ paratypes CW; 2 ♀ paratypes DASF) (depositories proposed by Dr. J. Stibick) (holotype lacks both antennae, both fore tibiae, left hind leg, right hind tibia and apex of left fore wing).

#### **Description.**

♂ (pl. 7 fig. 38, pl. 8 fig. 42), small. Face rather reclinate. Fastigium of vertex (pl. 9 fig. 47) thorn-like, apex acute, extending far beyond antennal scrobae, reaching third antennal segment (first segment of flagellum), in profile slightly upcurved. Pronotum short; dorsum flattened, weakly rounded laterally, "shoulders" distinct, anterior margin almost and posterior margin quite straight, both with weak median tubercle; lateral lobe about as long as high, lower margin slightly rounded, deepest point at or just before middle of length.

Flexed wings reaching distal end of proximal third of hind tibia. Fore wing narrow, margins about parallel, slightly tapering toward obliquely truncate apex. Stridulatory file (pl. 10 fig. 62) slightly arcuate and fusiform, 2.4 mm long, number of teeth 150, of which anterior 40 fine and covering anterior seventh of file length, other 110 sharp. Width of file reaching maximum 0.26 mm at end of anterior fourth, decreasing posteriorly to about half maximum width. Spacing of teeth slightly increasing posteriorly, comparatively more in anterior part. Mirror (pl. 10

fig. 67) about twice as long as wide, roughly elliptical, fold extending well over mirror, outline convex.

Fore and mid femora with 0—5 spines on anteroventral margin. All knee-lobes with one spine. Fore and mid tibiae with 2-5 dorsal spines on the anterior and 0-3 dorsal spines on posterior margin, no dorso-apical spines.

Cercus (pl. 9 fig. 57) slender, slightly incurved, tapering to a short tooth. Subgenital plate (pl. 9 fig. 51) very narrow, seven times as long as smallest width, apex divided by narrow, about parallel-sided incision into pair of narrow lobes with rounded tips, each with short stylus.

♀ (pl. 7 fig. 41, pl. 8 fig. 43). Apex of flexed wings reaching tip of ovipositor or almost so. The ovipositor slightly upcurved, comparatively short, reaching not quite middle of hind tibia. Subgenital plate wider than long, with slight median apical incision, lobes angulately rounded. Lower margin of ninth tergite extending over upper part of gonangulum (= valvifer), forming shallow groove.

General colour pale brown or pale green. Antennae more or less darkly annulated. Apex and dorsal side of fastigium of vertex, four longitudinal lines over occiput and lateral margins of pronotal dorsum dark brown; sometimes whole occiput, pronotal dorsum and cubito-anal areas of fore wing dark brown. Fore wing with more or less numerous scattered black dots, membrane partly transparent and slightly opaque. Pleurae and coxae with or without some black dots. Lower side of fore femur usually dark brown, fore tibia and mid leg of general colour. Hind femur between bases of knee-lobes, often inner lower margin and sometimes whole lower side, blackish brown. Hind tibia of general colour, lower side often dark brown. Spines brown, tips black, those of hind femur usually completely black.

Measurements: body ♂ 35, ♀ 36—38; fore wing ♂ 36, ♀ 36—41; hind femur ♂ 22 ♀ 24—26; ovipositor 18—20.

Distribution. Known only from the type-series, East New Guinea, Madang District: Kaironk area (map 2).

Discussion. The species is well-defined, although at a first glance it resembles *Segestidea acuminata* (Kästner). The latter species, known in the female sex only, differs in presence of fore and mid tibial dorso-apical spines, larger measurements, shorter fastigium of vertex and wider lobes of the female subgenital plate.\*

No previous records.

### ***Segestes brevipennis* spec. nov.**

(pl. 7 fig. 39, pl. 8 fig. 44, pl. 9 figs. 52, 58, pl. 10 fig. 63, map 2)

Material studied: ♂ holotype, labelled: Egemendora, J. Eyma leg., Nieuw Guinea Exp. K.N.A.G. 1939, mid Oct. 1939 (CW) (left mid leg lacking).

#### **Description.**

♂ (pl. 8 fig. 44), small. Fastigium of vertex thorn-like, extending well beyond antennal scrobae, just reaching apical margin of scape, slightly upcurved. Pronotal



dorsum flattened in the middle, slightly rounded laterally, "shoulder" well developed; anterior margin slightly convex, posterior margin straight, both margins with weak median tubercle. Pronotal lateral lobe as long as high, lower margin scarcely convex, angles rounded, deepest point about in the middle.

Flexed wings reaching distal end of proximal fourth of hind tibia. Fore wing with margins roughly parallel, scarcely tapering toward obliquely truncated apex; archidictyon well-developed. Stridulatory file slightly arcuate and fusiform (pl. 10 fig. 63), 2.0 mm long, number of teeth 71, of which anterior 17 fine, covering anterior seventh of file length, the other 54 sharp. Width of file strongly increasing in anterior seventh of file length, reaching there its maximum (0.35 mm), decreasing posteriorly to about half maximum width. Spacing of teeth increasing in anterior part. Mirror damaged (not figured), about as in *stibicki*.

Fore and mid femora with 2-3 spines on anteroventral margin. Fore tibia with 3 dorsal spines on anterior margin, posterior margin unarmed. Mid tibia with 2 dorsal spines on anterior and 6 dorsal spines on posterior margin. Fore and mid tibial dorso-apical spines lacking. All knee-lobes with one spine.

Cercus (pl. 9 fig. 58) slightly incurved, tapering apically to a short tooth. Subgenital plate (pl. 9 fig. 52) about six times as long as smallest width, apex divided by wide V-shaped incision into pair of lobes with truncate tips, in the middle of the latter a minute stylus.

General colour dark brown. Antennae slightly annulated pale and dark brown. Fore wing with cubito-anal areas and several scattered points and dots dark brown, hind margin narrowly yellowish brown. Lower side of all legs dark brown, especially of hind femur and hind knee. Spines with tips black.

♀. Unknown.

Measurements: body 34; fore wing 32; hind femur 21.

Distribution. Known only after the type, West New Guinea: Egemendora (map 2).

Discussion. The species comes near *stibicki* from which it is separated as indicated in the key. Further material is needed to establish the reliability of the differences mentioned.

No previous records.

### ***Segestes cornelii* spec. nov.**

(pl. 6 fig. 31, pl. 7 fig. 40, pl. 9 figs. 46, 50, 56, pl. 10 figs. 61, 66, map 2)

The species is named after my late father, Cornelis J. M. Willemse.

Material studied: ♂ holo-, 3♂ 4♀ paratypes, labelled: Kandep, West. Highl. Distr., New Guinea, 14.ii.1964, J. J. H. Szent-Ivany, on *Sach. robosium* and *Pandanus* (holo-, 1♂ 2♀ paratypes CW; 2♂ 2♀ paratypes DASF) (holotype lacks tips of antennae only).

#### **Description.**

♂ (pl. 6 fig. 31), large. Fastigium of vertex (pl. 9 fig. 46) thorn-like, apex acute,

reaching just beyond apical margin of scape, slightly upcurved. Pronotal dorsum slightly flattened in middle, slightly rounded laterally, anterior margin almost, posterior margin quite straight. Pronotal lateral lobe slightly longer than high, lower margin slightly convex, deepest point about in middle.

Flexed wings reaching almost middle, or usually distal end of proximal third of hind tibia. Fore wing wide, margins about parallel, slightly tapering toward a wide, obliquely truncated and rounded apex; archidictyon well-developed, transverse veins poorly developed. Stridulatory file (pl. 10 fig. 61) almost straight, 3.1—3.2 mm long, number of teeth 85—100, of which anterior 25—35 very fine and blunt in anterior seventh of file length, the other 60—70 sharp. Width of file strongly increasing in anterior part, reaching maximum 0.35—0.4 mm at end of proximal fifth of file length, slightly decreasing posteriorly to half maximum width. Spacing of teeth increasing in anterior seventh of file length, sharp teeth about regularly spaced. Mirror (pl. 10 fig. 66) elongate, less than twice as long as wide, trapezoidal, fold much extending over mirror, outline of fold convex, reaching about as far as postero-apical angle of mirror.

Fore and mid femora with 0—3 spines on anteroventral margin. All knee-lobes with one spine. Fore and mid tibiae with 1—6 dorsal spines on anterior and 0—2 on posterior margin, no dorso-apical spines.

Cercus (pl. 9 fig. 56) incurved, tapering apically to a short tooth on inner side of tip. Subgenital plate (pl. 9 fig. 50) rather three times as long as smallest width, apex divided by wide triangular incision into slightly narrower triangular lobes with obtusely pointed tips, the latter representing vestigial styli.

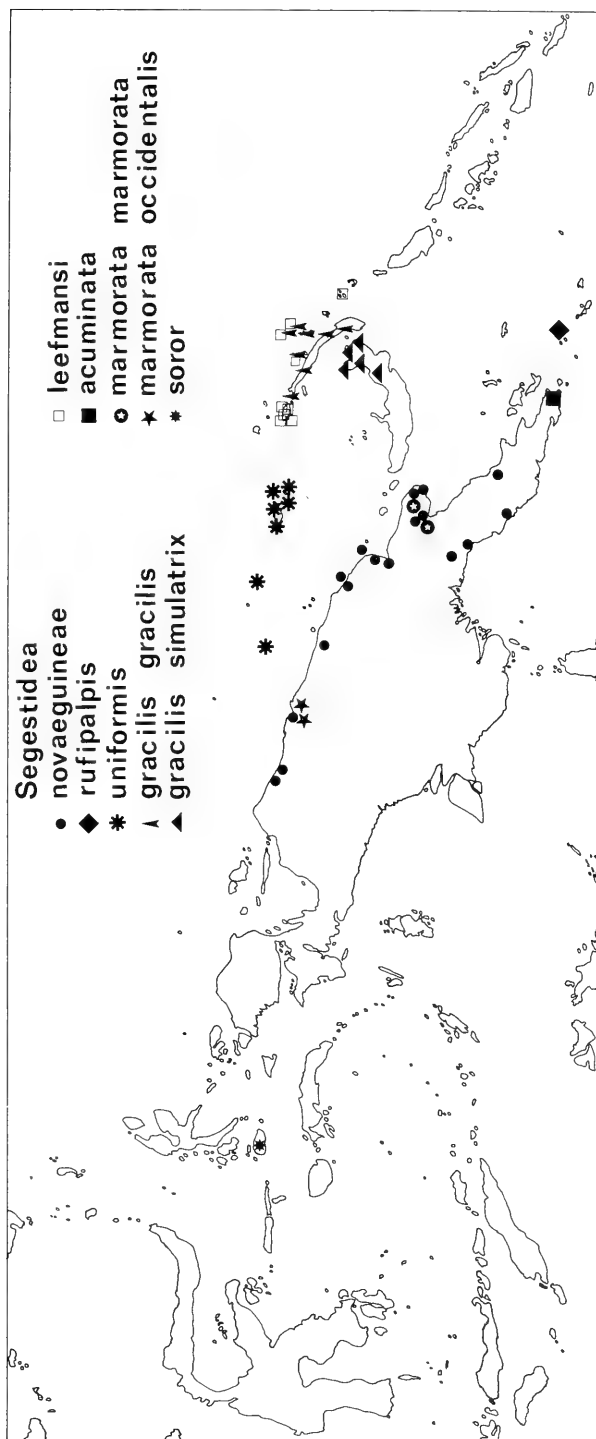
General colour pale and dark brown. Antennae annulated pale and dark brown. Pronotal dorsum sometimes darker brown, or only laterally so. Fore wing unicolorous or inconspicuously mottled dark brown, membrane infusate; hind margin sometimes narrowly bordered with pale or yellowish brown. Fore and mid legs of general colour, lower side of fore femur often dark brown. Hind femur of general colour with lower side between bases of knee-lobes or whole inner lower margin or whole lower side black. Hind tibia often dark brown from below, except apically. Spines of tibiae and knees brown, tips black, those of femora usually completely black. Tarsi from below dull dark brown.

♀ (pl. 7 fig. 40), slightly larger than male. Ovipositor very slightly upcurved, comparatively short, reaching distal end of proximal third of hind tibia and, in dorsal view, completely covered by flexed wings. Lower margin of ninth tergite slightly extending over gonangulum (= valvifer), forming shallow furrow. Subgenital plate much wider than long, with shallow median apical emargination, lobes widely rounded. General colour paler brown.

Measurements: body ♂ 49—53, ♀ 54—57; fore wing ♂ 57—60, ♀ 56—64; hind femur ♂ 34—36, ♀ 34—37; ovipositor 26—30.

Distribution. Known only from the type-locality, East New Guinea, Western Highlands District: Kandep (map 2).

Discussion. The species is well-defined. This species, together with *brevipennis* and *stibicki* forms the link between *Segestes* and *Segestidea*. The thorn-like fastigium of vertex, the flattened pronotal dorsum and the somewhat truncated



Map 3. Distribution of *Segestidea* species.

apex of fore wing are found also in *Segestidea marmorata* and *acuminata*. No previous records.

### **Segestidea I. Bolívar, 1903**

*Segestidea* I. Bolívar, 1903: 166.

*Eumossula* C. Willemse, 1957: 38 (type-species by monotypy: *Eumossula gracilis* C. Willemse, 1957).

Syn. nov.

Type-species (by Kirby, 1906: 359): *Segestidea princeps* I. Bolívar, 1903 (= *Segestidea novaeguineae* (Brancsik, 1897)).

*Segestidea*, as now understood in the key to the genera, is a natural group of species characterized by the presence of a posterior dorso-apical spine on fore and mid tibiae (text-fig. 1), in combination with the usual oblique course of Cu1 of the fore wing, i.e. vein reaching the hind margin of the fore wing or almost so at short distance from the wing-base (text-figs. 3, 6, 7).

Up to now, the following species were arranged under *Segestidea*:

*princeps* I. Bolívar, 1903

*marmorata* I. Bolívar, 1903

*punctipennis* I. Bolívar, 1903

*soror* Hebard, 1922

*hanoverana* C. Willemse, 1957

*insulana* C. Willemse, 1957

The generic distinction among Sexavae as considered in this paper, indicates that the following taxa also fit in *Segestidea*:

*Sexava femorata* C. Willemse, 1940

*Sexava leefmansi* C. Willemse, 1940

*Sexava uniformis* C. Willemse, 1940

*Segestes acuminatus* Kästner, 1934

*Sexava rufipalpis* C. Willemse, 1966

As will be pointed out, *Eumossula* C. Willemse, 1957, is synonymous with *Segestidea*. As a result, its single species, *Eumossula gracilis* C. Willemse, 1957, should be arranged under *Segestidea*.

Further study of the literature reveals that *Moristus novaeguineae* Brancsik, 1897, is synonymous with *Segestidea princeps*.

For convenience' sake, a survey is here given of all presently recognized species and subspecies in *Segestidea*, noting the new combinations and synonyms:

*Segestidea novaeguineae* (Brancsik, 1897), comb. nov. (from *Moristus*) = *Segestidea*

*princeps* I. Bolívar, 1903, syn. nov. = *Sexava femorata* C. Willemse, 1940, syn. nov.

*Segestidea punctipennis* I. Bolívar, 1903

*Segestidea soror* Hebard, 1922

*Segestidea leefmansi* (C. Willemse, 1940), comb. nov. (from *Sexava*) = *Segestidea*

*hanoverana* C. Willemse, 1957, syn. nov.

*Segestidea uniformis* (C. Willemse, 1940), comb. nov. (from *Sexava*) = *Segestidea*

*insulana* C. Willemse, 1957, syn. nov.

*Segestidea gracilis gracilis* (C. Willemse, 1957), comb. nov. (from *Eumossula*)

*Segestidea gracilis simulatrix* ssp. n.

*Segestidea rufipalpis* (C. Willemse, 1966), comb. nov. (from *Sexava*)

*Segestidea marmorata marmorata* I. Bolívar, 1903

*Segestidea marmorata occidentalis* ssp. n.

*Segestidea acuminata* (Kästner, 1934), comb. nov. (from *Segestes*).

### Key to the species and subspecies of *Segestidea*

1. Philippine Is. (known only after ♀ holotype, body 38 mm, fore wing 29 mm, ovipositor 21 mm; fore wing with sparse brown dots) . . . *punctipennis* I. Bolívar
- The Moluccas, New Guinea, Bismarck Archipelago . . . . . 2
2. Fastigium of vertex thorn-like, apex acute, reaching at least apical margin of scape . . . . . 3
- Fastigium of vertex with apex obtusely pointed, shorter, not reaching apical margin of scape . . . . . 5
3. Fastigium of vertex reaching pedicel (second antennal segment); fore wing wider (known only from ♀ holotype from East New Guinea: Milne Bay; may be synonymous with nominate *marmorata* I. Bolívar) . . . *acuminata* (Kästner)
- Fastigium of vertex reaching first segment of flagellum (third antennal segment); fore wing narrower . . . . . 4
4. Male stridulatory file about 3.0 mm long with about 100 teeth (of which 75 are sharp and apparently functional) (pl. 17 fig. 113) (East New Guinea: Morobe District) . . . . . *marmorata marmorata* I. Bolívar
- Male stridulatory file of same length, but with about 200 teeth (of which about 175 are sharp and apparently functional) (pl. 17 fig. 114) (West New Guinea: Hollandia area) . . . . . *marmorata occidentalis* ssp. n.
5. Proximal part of lower and inner side of hind femur solid black or blackish brown . . . . . 6
- This part of hind femur not black . . . . . 7
6. Fore wing with solid blackish brown flecks; knee-lobes with one spine (the Moluccas: Obi) (known only from the two type specimens) . . . *soror* Hebard
- Fore wing unicolorous or slightly mottled dark brown; knee-lobes usually with two spines (Bismarck Archipelago: New Ireland District) . . . . . *leefmansi* (C. Willemse)
7. Apical part of hind tibia, over a distance as long as hind tarsus, blackish, except for upper side; proximal part of outer side of hind femur with a series of small, black spots, or sometimes with a single large spot, exceptionally without any spot; ventral spines of hind femur unusually widened basally, almost triangular (East New Guinea, extending into northeastern part of West New Guinea) . . . . . *novaeguineae* (Brancsik)
- Hind tibia unicolorous over whole length; outer side of hind femur always without solid black spots; ventral spines of hind femur hook-shaped as usual . . . . . 8
8. Lower margin of pronotal lateral lobe angulate, deepest point about at distal

- third; male stridulatory file as in pl. 16 fig. 108 (East New Guinea: Louisiade Archipelago, Misima I.) . . . . . *rufipalpis* (C. Willemse)
- Lower margin of pronotal lateral lobe more convex, deepest point about in the middle; male stridulatory file not as in pl. 16 fig. 108 (Bismarck Archipelago) . . . . . 9
9. Wings longer, reaching about the middle of hind tibia; ovipositor not extending beyond apex of flexed wings (pl. 11 fig. 74, pl. 12 figs. 75, 76) (Admiralty Is. or Manus District) . . . . . *uniformis* (C. Willemse)
- Wings shorter, reaching about distal end of proximal fourth of hind tibia; ovipositor extending far beyond apex of flexed wings (pl. 12 figs. 77—79, pl. 13 figs. 80—82) (New Ireland and New Britain) . . . . . 10
10. Anterior part of male stridulatory file narrow, maximum width reached at the middle of file length (pl. 16 fig. 110) (New Ireland District) . . . . . *gracilis gracilis* (C. Willemse)
- Anterior part of male stridulatory file wider, maximum width reached far before the middle of file length (pl. 16 fig. 111) (East New Britain District) . . . . . *gracilis simulatrix* ssp.n.

***Segestidea novaeguineae* (Brancsik, 1897) comb. nov.**

(text-figs. 3, 6, 7, pl. 11 figs. 68—71, pl. 15 figs. 91, 99, pl. 16 fig. 107, pl. 17 fig. 115, map 3)

*Moristus novaeguineae* Brancsik, 1897: 81.

*Sexava novaeguineae*; Kirby, 1906: 359.

*Sexava coriacea novaeguineae*; Karny, 1926: 184.

*Segestidea princeps* I. Bolívar, 1903: 167; Kästner, 1934: 53. **syn. nov.**

*Sexava femorata* C. Willemse, 1940: 83, figs. 17, 18; 1961: 109, fig. 14; F. Willemse, 1966: 49 (except 1 ♀ Manam I.); Lloyd & Gurney, 1975: 47. **syn. nov.**

*Sexava* species A: O'Connor, 1959: 122.

Material studied: ♀ holotype of *Sexava femorata*, labelled: Halmaheira, *Sexava femorata* n.sp. Det. C. Willemse (CW) (lacking parts of both hind tarsi).

Additional material: Gulf District of Papua, Kerema, ii.1962, sitting on branch of *Coffea canephora* (1 ♀ CW); Gulf distr., Purari Village, Pawaia no. I., ix—x.1'70, J. I. Menzies (2 ♀ DASF); Port Moresby, viii.1969 (1 ♀ CW); Northern District, Popondetta, Casey's Plantation, xi.1960, G. S. Dunn, under the bark of bush trees (1 ♀ DASF); Popondetta, season 1964, B. J. Brock (1 ♂ 1 ♀ BMNH); Boana Mission, Huon Pen., 900 m, 4—5.ix.1956, E. J. Ford Jr., *Sexava femorata* Will. det. C. Willemse (1 ♂ BPBM); Bubia via Lae, 12.vii.1960, A. Catley, feeds on coconut foliage and on Manila hemp foliage (*Musa textilis*), often parasitized by *Stichotrema dallatorreana* Hofeneder (Strepsiptera) (7 ♂ 9 ♀ CW) (partly labelled *Sexava femorata* Will., det. C. Willemse); Madang District, Bogia, i.1960, J. Cox, on coconut fronds (1 ♂ DASF); Manam I., Baliau Village, 26.xi.1960, J. I. Cox, *Sexava femorata* Will. det. C. Willemse (2 ♂ 7 ♀ CW); Karkar I., ii.1969, G. R. Forbes (1 ♂ DASF); Karkar I., Kulili Plantation, 20 & 24.ix.1958, J. H. Ardley, ex coconut palms (4 ♂ DASF); Hollandia, viii.1910, Dr. P. N. v. Kampen, Ned. Nw.

Guinea Exp. 1911 (4♂ 3♀ RNH); Hollandia, 24.vii.1938, L. J. Toxopeus, Neth. Ind. Amer. New Guinea Exp. 1938—39 (1 ♂ u RNH); Maffin Bay, vi.1944, E. S. Ross (1♂ 1♀ CAS).

The venation of the fore wing and the presence of fore and mid tibial dorso-apical spines of the holotype and other material studied of *Sexava femorata* agree with *Segestidea* as here understood. The species is well-defined by a number of characters, some quite typical. Several of these characters, including the typical ones, are mentioned in the description of Bolívar's *Segestidea princeps*: "Antennae — late albido-annulatae — Caput pone oculos fascia pallida obliqua, parum distincta — Pronotum — lobis deflexis inferne pallidis — Elytra — venis transversis campi postradialis elevatiusculis, prope venas radiales subcallosus, flavis — Femora — postica — subtus carnea, extus tertia parte basali maculis fuscis seriatis ornata, carinis inferioribus — spinis validis armata — Tibiae posticae apice nigra. Tarsi atri." Also the measurements and the locality of *princeps* (Simbang, Huon Gulf) are covered by *femorata* material before me. Unfortunately the holotype (unique ♀) (TMA) has been lost (Steinmann, in litt. 3.xii.1975; V. Llorente, in litt. 9.i.1976). Moreover, the species was badly known, a second female only having been recorded by Kästner (1934: 53) who gave no further comments except for its measurements. Because the typical characters of Bolívar's species fit only *femorata*, both taxa should be considered synonymous.

A similar case offers the comparison of the present material with Brancsik's *Moristus novaeguineae*. That species was known only from the female holotype from Friedrich Wilhelmshafen (TMA). Again the holotype has been lost (Steinmann, in litt. 3.xii.1975) and further taxonomically reliable records are not known. The species was discussed by Karny (1926: 184). Although that author neither had the type nor other material before him, he considered it a variety of *Sexava coriacea*: "da sie [*novaeguineae*] sich von dieser [*coriacea*] nach der Original Beschreibung im wesentlichen eigentlich nur durch etwas geringere Dimensionen und die die Elytren nicht überragende Legeröhre unterscheidet". However, Karny's conclusion is not correct. In Brancsik's short description it is said: "tibiis posticis apice tarsisque omnibus subtus fuscus". This feature disagrees with any *Sexava* species and fits only *princeps* = *femorata*. Also the measurements of *novaeguineae* agree with the latter rather than with *Sexava nubila* or *coriacea*. Moreover, the type-locality of Brancsik's species is within the range of *princeps* = *femorata* and not by far within that of *Sexava*. When comparing the green coloured specimens before me with Redtenbacher's monography of the Mecopodinae (1892: 201), as most probably did Brancsik (1897), the context of the description of *novaeguineae* is perfectly clear. Based on so much evidence, I propose to synonymize *Sexava femorata* and *Segestidea princeps* with *Moristus novaeguineae*. The last, being the oldest available name, is given priority and the generic assignment leads to the new combination: *Segestidea novaeguineae* (Brancsik).

#### Redescription.

♂ (pl. 11 fig. 68), large. Fastigium of vertex obtusely pointed, often with shallow median furrow and slightly fissate apex, reaching to, or slightly extending beyond,

antennal scrobae, not by far to apical margin of scape. Pron slightly flattened medially, strongly rounded laterally, anterior margin slightly, posterior margin less convex to almost straight, "shoulders" indistinct. Pronotal lateral lobe about as long as high, lower margin angulate, deepest point distally of the middle of lobe length, this point sometimes produced posteriorly.

Flexed wings reaching distal end of proximal third to middle of hind tibia. Fore wing wide, long, margins in proximal half about parallel, beyond middle or in distal third evenly tapering toward narrowly rounded apex (text-fig. 3); costal area with numerous parallel obliquely transverse veins, most of these and the transverse veins of radial and medial areas, slightly incrassate; archidictyon well-developed; membrane slightly opaque. Venation of bases of left and right fore wing as in text-figs. 6 and 7. Stridulatory file (pl. 16 fig. 107) fusiform, scarcely arcuate, 4.2—5.0 mm long, number of teeth 175—190 of which anterior 40—50 fine and less sharp, other 135—150 sharp and apparently functional. Width of file increasing to maximum 0.5—0.6 mm in anterior third of file length, but slightly decreasing again posteriorly. Spacing of teeth about regular except for more closely set anterior ones. Mirror (pl. 17 fig. 115) one-and-a-half times as long as wide or shorter, about trapezoid; fold strongly inflated in basal half, extending well over mirror, outline convex basally, running obliquely toward postero-apical angle.

Fore and mid femora usually unarmed, sometimes with 1—3 spines in apical part of anteroventral margin. Hind femur, except near base, with series of strong ventral spines on both margins, spines widened basally and almost triangular in profile. All knee-lobes with two spines, sometimes posterior or seldom also anterior knee-lobe of mid leg and more often of fore leg, with one spine. Fore tibia with 0—1, mid tibia with 4—6 dorsal spines on posterior margin, both tibiae with a posterior dorso-apical spine.

Cercus (pl. 15 fig. 99) incurved, tapering apically to a short, hook-shaped tooth. Subgenital plate (pl. 15 fig. 91) 5—6 times as long as smallest width, margins about parallel, apex divided by V-shaped or parabolic incision into pair of lobes, tips of the latter obliquely truncated and with styli.

General colour bright green or brown. Antennae widely and distinctly annulated pale yellow and dark brown, except basally. Palpi of general colour, yellowish or orange. Often whitish fascia from behind eye, extending over genae, lower margin of pronotal lateral lobe and pleurae. Outer side of hind femur often with pale and dark transverse stripes, basal third with a series of solid black or dark brown spots, sometimes fused into one or few larger ones. Lower side of hind femur of general colour or reddish. Apical part of hind tibia, for a distance about as long as hind tarsus, black or blackish brown, dorsally usually paler brown or of general colour. All tarsi from below dull black or blackish brown. Spines of femora black, those of hind femur usually with basal part reddish brown. Spines of tibiae black, except for dorsal ones of hind tibia, which are of general colour with tips black.

♀ (pl. 11 figs. 69—71) larger than male. Ovipositor straight or almost so, reaching distal end of proximal third to middle of hind tibia, not or very slightly extending beyond apex of flexed wings. Subgenital plate wide, triangular, with median apical emargination and rounded lobes. Coloration as in male.



Variation. Measurements vary, but comparative length of wings and ovipositor are about equal. The contrast between the generally bright green or dark coloured specimens is conspicuous. The black spots of the basal third of the outer side of the hind femur are lacking in very few specimens.

Measurements: body ♂ 50—62, ♀ 56—62; fore wing ♂ 58—70, ♀ 75—88; hind femur ♂ 39—45, ♀ 46—55; ovipositor 35—42.

Distribution. The range covers the eastern half of the mainland of New Guinea, extending onto some islands near the coast and into the northern part of western New Guinea (map 3).

Localities: West New Guinea: Maffin Bay; Takar (O'Connor, 1959); Hollandia. East New Guinea: East Sepik District: Maprik (O'Connor, 1959); Madang District (O'Connor, 1959); Friedrich Wilhelmshafen (Brancsik, 1897); Stephansort (Kästner, 1934); Bogia; Manam I. (O'Connor, 1959), Baliau Village (F. Willemse, 1966); Karkar I. (O'Connor, 1959), Kulili Plantation; Morobe District: Simbang (Bolívar, 1903); Sattelberg; Bubia (F. Willemse, 1966); Boana Mission (C. Willemse, 1961); Northern District: Popondetta, Casey's Plantation; Central District: Port Moresby; Gulf District: Kerema; Purari Village.

Discussion. The species is well-defined. Easily recognizable are the blackish apical part of the hind tibia, the black dots on the basal outer side of the hind femur and the strong spines of the hind femur. The locality label of the holotype of *femorata* reads "Halmaheira", which appears doubtful. The material recorded under *Sexava* species A by O'Connor (1959) is not at hand. However, his records can refer only to *novaeguineae* and are included in the locality list and on the distribution map.

### ***Segestidea rufipalpis* (C. Willemse, 1966) comb. nov.**

(pl. 11 figs. 72, 73, pl. 15 figs. 92, 100, pl. 16 fig. 108, pl. 17 fig. 116, map 3)

*Sexava rufipalpis* C. Willemse, 1966: 1, figs. 1, 2; F. Willemse, 1966: 49.

Material studied: type-series, ♂ holo-, ♀ allo-, 2♂ paratypes, labelled: Liak Village, Misima Island, Milne Bay District, of Papua, Feb. 1962; feeding on the foliage of *Cocos nucifera*, coll. D. I. Murrie, *Sexava rufipalpis* sp.n. Det. C. Willemse 1962, appropriate type-labels (CW) (holotype lacks right antenna, right fore leg, both mid tibiae and tips of both hind tarsi).

For a general description, compare original one. Differs from the type-species as follows.

More robust but not larger (pl. 11 figs. 72, 73). Apex of flexed wings not reaching beyond proximal third of hind tibia and almost beyond tip of ovipositor. Fore wing with apex narrowly rounded, almost pointed. Male stridulatory file (pl. 16 fig. 108) distinctly fusiform, almost straight, about 4 mm long, number of teeth 95—105 of which anterior 15—20 very fine, blunt, closely set and weakly sclerotized, arranged over anterior ninth of file length, the other 80—90 sharp and strongly sclerotized. Width of file strongly increasing in anterior ninth, from there

but slightly and reaching maximum of 0.5 mm at distal end of anterior fourth of file length, decreasing posteriorly to about one-fourth of maximum width. Spacing of nine anterior teeth very close, of remaining part of file about regular and much more widely spaced than in type-species. Mirror (pl. 17 fig. 116) less trapezoid, more elongate-elliptical, fold extending less over mirror and less inflated. Spines of hind femur not widened basally but hook-like as usual. Male cercus and subgenital plate as in pl. 15 figs. 92, 100.

General colour green. Antennae scarcely annulated. Palpi orange. Whitish fascia of head and thorax scarcely indicated. Pronotal dorsum, on each side, with a minute black point in the impressed posterior transverse sulcus. Legs, including apical part of hind tibia and outer side of hind femur and tarsi, of general colour. Dorsal spines of hind tibia orange brown, tips black, other spines of legs completely black or almost so.

Measurements: body ♂ 47—52, ♀ 60; fore wing ♂ 57—64, ♀ 70; hind femur ♂ 39—40, ♀ 48; ovipositor 39.

Distribution. Known only from the type-locality, Papua, Milne Bay District: Louisiade Archipelago, Misima I. (map 3).

Discussion. The species is well-defined. The male stridulatory file is quite characteristic. The shape of the pronotal lateral lobe and the male abdominal terminalia are much as in *novaeguineae*.

### ***Segestidea uniformis* (C. Willemse, 1940) comb. nov.**

(pl. 11 fig. 74, pl. 12 figs. 75, 76, pl. 15 figs. 93, 101, pl. 16 fig. 109, pl. 18 fig. 117, map 3)

*Sexava uniformis* C. Willemse, 1940: 81, figs. 19, 20 (only Lou I.).

*Segestidea insulana* C. Willemse, 1957: 41, pl. 4 right; 1961: 111 (only Los Negr[it]os); F. Willemse, 1966: 48 (only paratypes of *insulana* and Wululu I.). **syn. nov.**

Material studied: ♀ holotype of *Sexava uniformis*, labelled: Lou II. '32, coll. Böhler, *Sexava* n. sp. det. Karny, *Sexava uniformis* nov. sp. Det. C. Willemse, Type (NMB) (discoloured, both fore legs, right middle leg and left fore wing lacking).

Type-series of *Segestidea insulana*: ♂ holotype, labelled: New Guinea Territory of Papua, Pak Island, 1954, T. H. Ardley, *Segestidea insulana* nov. spec. det. C. Willemse, type (BMNH); paratypes: similar locality label (1♂ 1♀ BMNH; 1♀ CW); Lou I., 1954, T. H. Ardley (1♂ 1♀ BMNH); Lorengau Manus I., 1954, T. H. Ardley (1♂ CW; 1♀ BMNH) (with appropriate identification and type-labels).

Additional material: Manus District, 24—28.ii.1974, J. Pippett (1♂ DASF); Manus District, Sala Plantation, 4.iii.1954, J. Ardley (1♀ DASF); Manus I., 5.v.1932, J. L. F. (1♂ 2♀ BMNH); Manus, 1932, N. E. H. Caldwell (1♂ BMNH); Manus I., Lei Village near Lorengau, 29.vi.1956, J. Szent-Ivany, feeding on fronds of coconut palms (1♂ 1♀ DASF); Manus I., Tulo Plantation N. coast, 19.i.1962, on *Cocos nucifera*, J. Szent-Ivany & P. Hermann (3♂ DASF); Manus I., Bundalis R. C. Mission, plantation N.coast, 19.i.1962, on mature coconuts, brought down by smoke, J. Szent-Ivany & P. Hermann (2♂ DASF); Los Negros Is., Momote

Airstrip, 26.ii.1960, defol. young coconut palms, J. Szent-Ivany (1♂ DASF); Los Negros, xi.1945, Wagner & Grether, *Segestidea insulana* Will. det. C. Willemse (1♂ BPBM); Pak I., 7.i.1971, P. R. Jones, on coconuts (3♂ 4♀ DASF); Hermit Is., Maron I., 10.vii.1961, ex coconut palms, J. H. Ardley (5♂ 5♀ CW); Wululu Isl., Agita Plantation, ix.1960, Rede Lean, severe damage to coconut foliage, *Segestidea insulana* Will. det. C. Willemse (6♂ 1♀ CW).

*Sexava uniformis* was described after two females, the holotype from Lou I., the paratype from Rook I. The latter represents another species and is discussed under *gracilis simulatrix*. Comparison of the holotype of *uniformis*, the type-series of *insulana* and other material at hand reveals clearly that they belong to one species, to be assigned to *Segestidea*.

For a general description the reader is referred to the original descriptions of *Sexava uniformis* and *Segestidea insulana*. The species differs from the type-species as follows.

Smaller, more slender (pl. 11 fig. 74, pl. 12 figs. 75, 76). Pronotal lateral lobe narrower, lower margin obtusely angulate, deepest point about in the middle. Flexed wings reaching middle of hind tibia or almost so, in dorsal view covering ovipositor completely. Ovipositor straight, tip reaching distal end of proximal third of hind tibia or slightly longer. Fore wing much narrower, comparatively less tapering toward comparatively more widely rounded apex; archidictyon less well-developed; transverse veins in costal area less numerous and less regular, not incassate; membrane more or less transparent. Male stridulatory file (pl. 16 fig. 109) fusiform, slightly arcuate, 3.4–4.0 mm long, number of teeth 130–140, of which anterior 35–50 fine, less sharp, and others (at least 85–95), sharp and apparently functional. Width of file increasing and reaching maximum 0.48–0.50 mm at distal end of anterior third of file length, slightly decreasing again posteriorly to about half maximum width. Spacing of teeth increasing in anterior third, functional teeth about regularly set. Mirror (pl. 18 fig. 117) about twice as long as wide, elongate-elliptical, fold distinctly less extending over mirror and but weakly inflated, outline straight and about parallel to hind margin of wing. Number of spines on legs about as in type-species, ventral spines of hind femur not widened, but hook-like as usual. Male cercus shorter (pl. 15 fig. 101) and very slightly incurved apically. Male subgenital plate (pl. 15 fig. 93) narrow, lateral margins often slightly concave, margins of V-shaped apical incision often slightly crenulated, styli comparatively longer and slightly incurved.

General colour green or brown. Antennae not or scarcely annulated. Head, thorax, wings and all legs of general colour. Fore wing sometimes with hind margin narrowly dark brown or yellowish. Spines of legs of general colour, tips black. Tarsi from below dull dark brown.

Measurements: ♂ 43–52, ♀ 42–57; fore wing ♂ 57–65, ♀ 62–74; hind femur ♂ 32–41, ♀ 34–44; ovipositor 26–33.

Distribution. As far as known, the range covers the north-western Bismarck Archipelago: Admiralty Is. (Manus District) (map 3).

Localities: Manus I.: Lorengau (C. Willemse, 1957); Lei Village; Tulo Plantation; Bundalis R. C. Mission; Sala Plantation; Lou I. (C. Willemse, 1940; 1957);

Pak I. (C. Willemse, 1957); Los Negros I. (C. Willemse, 1961), Momote Airstrip; Hermit Is., Maron I.; Wululu Is., Agita Plantation (C. Willemse, 1966).

**Discussion.** The species is well-defined, but the characters are not as easily recognizable as in some other species of the genus. Confusion is possible with nominate *Segestidea gracilis* and its subspecies *simulatrix*, and with *Segestes decoratus*. Distinction from the latter is discussed under that species. Both subspecies of *gracilis* have shorter wings and longer ovipositor, the latter extending far beyond the apex of the flexed wings (pl. 12 figs. 77—79, pl. 13 figs. 80—82). Moreover the lower margin of the pronotal lateral lobe is more convex, the male cercus more incurved (pl. 15 figs. 102, 103), the male subgenital plate wider (pl. 15 figs. 94, 95), and the styli shorter. The male stridulatory file in nominate *gracilis* has a quite different shape (pl. 16 fig. 110), while the file in *simulatrix* is less arcuate and differs in slightly wider spacing of the teeth (pl. 16 fig. 111).

***Segestidea gracilis* (C. Willemse, 1957) comb. nov.**

Among the material before me, two taxa can be recognized, based on consistent differences in the stridulatory file, as indicated in the key above. This may be evidence of genetic discontinuity in which case the taxa should be considered species. However, by lack of more supporting evidence, I prefer to consider them subspecies. One occurs in New Ireland and agrees with *gracilis*, the other subspecies is known from New Britain and named *simulatrix* ssp.n.

***Segestidea gracilis gracilis* (C. Willemse, 1957) comb. nov.**

(pl. 12 figs. 77—79, pl. 15 figs. 94, 102, pl. 16 fig. 110, pl. 18 fig. 118, map 3)

*Eumossula gracilis* C. Willemse, 1957: 37, figs. 1—3, pl. 2; 1958: 122 (only New Ireland); F. Willemse, 1966: 48 (do.).

*Segestidea insulana*; C. Willemse, 1961: 110 (only New Ireland); F. Willemse, 1966: 48 (do.).

**Material studied:** type-series of *Eumossula gracilis*, ♂ holo-, 1♂ 1♀ paratypes, labelled: New Guinea, Terr. of Papua, New Ireland, 1954, J. H. Ardley, *Eumossula gracilis* n.g. n.sp. Det. C. Willemse, appropriate type-labels (holo-, 1♂ paratype BMNH; 1♀ CW) (holotype lacks right antenna and some claws).

**Additional material** (all New Ireland District): Lihir I., Londolovit Plantation, on coconut fronds, 20.vii.1955, J. Szent-Ivany (3♂ CW); Lihir Group, Masahet I., on coconut palms, 21.vii.1955, J. Szent-Ivany (2♂ 2♀ CW); Lihir Group, Mahur I., on coconut palms, 22.vii.1955, J. Szent-Ivany (1♂ 2♀ CW); SW New Ireland, Gilingil Plantation, 2 m, 17.vii.1956, J. L. Gressitt (1♂ CW; 1♂ BPBM) (part of all this material with label: *Segestidea insulana* Will. Det. C. Willemse); New Ireland, Tigak D.A.S.F., 1. viii.1971, on coconut, J. Sumbak (1♀ DASf); Tabar I., Teripax Plantation, 23.vii.1955, on *Cocos nucifera*, J. Szent-Ivany (1♂ DASf); Lihir Group, Lataul Village, 15.xi.1968, D. F. O'Sullivan (1♂ DASf); New Ireland District, Namatanai, Matakan Plantation, 15.iii.1965, on *Theobroma cacao*, J. M. Adams

(1♂ 1♀ DASF); New Ireland District, Maramakas Plantation, 7.ii.1954, J. H. Ardley (1♂ DASF).

A study of the type-series and other available material reveals clearly that the monotypic *Eumossula* perfectly fits *Segestidea* and that its species, *gracilis*, is well-defined.

For a general description the reader is referred to the original one. The species differs from the type-species as follows.

Smaller (pl. 12 figs. 77—79). Lower margin of pronotal laterâ lobe slightly convex, not at all angulate. Wings shorter, in flexed position extending just beyond hind knee, not beyond proximal fourth of hind tibia, not by far reaching tip of ovipositor. Fore wing much narrower, slightly tapering toward narrowly rounded apex; archidictyon well-developed; transverse veins less numerous, less regular and not incrassate. Male stridulatory file (pl. 16 fig. 110) narrowly fusiform, slightly arcuate, 3.8—4.2 mm long, number of teeth 156—175 of which at least 50—70 cover the attenuated, narrow anterior third of file length, while others (about 100) are arranged over remainder of file. Width of file increasing but slightly all over anterior half, just before or in middle of file length increasing more abruptly, reaching maximum of 0.4—0.5 mm and decreasing again slightly in posterior fourth of file. Spacing of teeth slightly and gradually increasing in anterior half, from there slightly decreasing posteriorly. Mirror (pl. 18 fig. 118) wide elliptical, fold not strongly inflated, outline of the latter almost straight of slightly sinuate and but moderately extending over mirror. Number of spines of legs as in type-species. Ventral spines of hind femur hook-like, as usual. Male cercus (pl. 15 fig. 102) shorter, more robust. Male subgenital plate (pl. 15 fig. 94) comparatively shorter, about four times as long as smallest width. Ovipositor long, reaching middle of hind tibia or almost so, upper margin straight.

General colour pale green or brown. Antennae not or scarcely annulated. Head, thorax, fore wings and legs of general colour, spines with tips black.

Measurements: body ♂ 47—54, ♀ 48—59; fore wing ♂ 48—54, ♀ 54—63; hind femur ♂ 37—42, ♀ 40—44; ovipositor 36—40.

Distribution. The range of the nominate subspecies covers the New Ireland District of the Bismarck Archipelago (map 3).

Localities: New Ireland (C. Willemse, 1957); Giingil Plantation (C. Willemse, 1961; F. Willemse, 1966); Maramakas Plantation; Namatanai, Matakan Plantation; Tigak; Lihir Is., Lataul Village; Londolovit Plantation (C. Willemse, 1958; F. Willemse, 1966); Masahet I. (C. Willemse, 1958; F. Willemse, 1966); Mahur I. (C. Willemse, 1958; F. Willemse, 1966); Tabar I., Teripax Plantation.

Discussion. The nominate subspecies is characterized by short wings, long ovipositor and the shape of the male stridulatory file. As to the latter, it is noted that this character is rather uniform throughout the studied males of nine different localities.

Distinction with *Segestidea uniformis* and *Segestes decoratus* is discussed under these species.

***Segestidea gracilis simulatrix* subsp. nov.**

(pl. 13 figs. 80—82, pl. 15 figs. 95, 103, pl. 16 fig. 111, pl. 18 fig. 119, map 3)

*Sexava uniformis* C. Willemse, 1940: 82, figs. 19—20 (Rook I. only).*Segestidea insulana*; C. Willemse, 1961: 110 (New Britain only); F. Willemse, 1966: 48 (do.).*Eumossula gracilis*; C. Willemse, 1958: 122 (New Britain only); F. Willemse, 1966: 48 (do.).

Material studied: ♂ holotype, labelled: New Britain, Gazelle Peninsula, Lowl. Agr. Exp. Station Keravat, 26.v.1954, J. Szent-Ivany, on the fronds of African oil-palms *Elea guineensis*, *Eumossula gracilis* Will. Det. C. Willemse 1958 (CW) (both antennae, left fore tibia and parts of tarsi lacking).

Paratypes: similar to holotype (1 ♀ CW), similar locality and identification label, viii.1958, G. S. Dunn, on *Cocos nucifera* (1 ♂ 2 ♀ CW), similar locality, 60 m, 11.ix.1955, J. L. Gressitt, *Segestidea insulana* Will. Det. C. Willemse (1 ♂ 2 ♀ BPBM; 1 ♀ CW); New Britain, Gazelle Peninsula, Bainings St. Paul's, 350 m, 9. ix. 1955, J. L. Gressitt, *Segestidea insulana* Will. Det. C. Willemse (13 ♂ 4 ♀ BPBM; 1 ♂ CW); New Britain, Gazelle Peninsula, Malaguna, 4.iii.1971, feeding on foliage of *Cocos nucifera*, A. Gameta & J. Guguna (3 ♂ 2 ♀ DASf); New Britain, Gaulim Peninsula, 23.v.1955, *Segestidea insulana* Will. det. C. Willemse (1 ♀ BPBM); New Britain, Sio, N. coast, 600 m, 24.vii.1956, *Segestidea insulana* Will. det. C. Willemse (1 ♂ BPBM); New Britain, Ti, Nakagai, 28.vii.1956, E. J. Ford, *Segestidea insulana* Will. det. C. Willemse (1 ♂ BPBM); E. N. B. District, 30.xii.1974, on coconut leaf, D. Tago (1 ♀ DASf); New Britain, Kokope East, Gunanua Plantation, 27.iv.1968, on oil palm, R. Abijah (1 ♀ DASf); East New Britain, Sumsum Plantation, 31.iii.1971, *Cocos nucifera*, D. F. O'Sullivan (1 ♀ DASf); Rook I., Umboi, 1930, H. Hediger, *Sexava uniformis* nov. spec. Det. C. Willemse, cotype (1 ♀ NMB).

**Description.**

Differing from nominate subspecies as follows (pl. 13 figs. 80—82). Male stridulatory file (pl. 16 fig. 111) slightly fusiform, scarcely arcuate, 3.8—4.2 mm long, number of teeth 117—139 of which anterior 20—40 fine and less sharp covering anterior fifth of file length, other teeth, about 100, arranged over remaining of file. Width of file stronger, increasing in anterior fifth, reaching maximum of 0.4—0.5 mm at distal end of proximal third of file length, from there slightly decreasing posteriorly. Spacing of teeth increasing in anterior third, about regular in remaining of file. Mirror (pl. 18 fig. 119) slightly more elongate. Male cercus (pl. 15 fig. 103) slightly more incurved.

General colour green or brown, sometimes slightly mottled darker brown, especially in fore wing.

Measurements: body ♂ 46—52, ♀ 53—59; forewing ♂ 45—50, ♀ 53—58; hind femur ♂ 32—36, ♀ 38—40; ovipositor 36—38.

Distribution. As far as known confined to New Britain (and Rook I. ?) (map 3).

Localities: East New Britain: Sumsum Plantation; Malaguna; Kokopo, Gunanua Plantation; Bainings St. Paul's (C. Willemse, 1961; F. Willemse, 1966); Keravat

Lowlands Agric. Exper. Station (C. Willemse, 1958, 1961; F. Willemse, 1966); New Britain: Ti, Nakagai; Sio, N. coast; Gaulim Peninsula; Rook I.

**Discussion.** This subspecies is characterized by its resemblance with the nominate subspecies in combination with its clearly distinct male stridulatory file. As in the nominate subspecies, it is noted that the file of the studied males from five different localities is quite uniform. Whether the slight differences of the male cercus, subgenital plate and mirror (pl. 15 figs. 95, 103, pl. 18 fig. 119) are reliable characters, is not certain by lack of sufficient material. The paratypic *Sexava uniformis* female from Rook I. is discoloured and badly damaged. Without the male, identification is uncertain, although it can be said that the specimen disagrees with *uniformis* and *Segestes decoratus*. Judging from the length of the wings and the ovipositor and the shape of the pronotal lateral lobe, it fits *gracilis*. As to the range of the subspecies of the latter, *simulatrix* may be expected to occur in Rook I. rather than the nominate form.

Distinction between *gracilis simulatrix*, *Segestidea uniformis* and *Segestes decoratus* is discussed under the last two species.

***Segestidea leefmansi* (C. Willemse, 1940) comb. nov.**

(pl. 13 figs. 83, 84, pl. 14 fig. 85, pl. 15 figs. 96, 104, pl. 16 fig. 112, pl. 18 fig. 120, map 3)

*Sexava leefmansi* C. Willemse, 1940: 83, fig. 21—22.

*Segestidea hanoverana* C. Willemse, 1957: 39, pl. 3, 4 left; F. Willemse, 1966: 48. **syn. nov.**

**Material studied:** type-series of *Sexava leefmansi*: ♂ holotype, labelled: La-wongai N.H. xi.31 coll. Bühler, *Sexava* sp. n. det. H. Karny, *Sexava leefmansi* nov. sp. adet. C. Willemse, type (discoloured, left fore leg and right fore tibia lacking); paratypes: similar labels, cotype (1♂ 1♀); Namaoroso N.H. xi.31 coll. Bühler, similar identification labels, cotype (1♂ 1♀) (all NMB).

Type-series of *Segestidea hanoverana*: ♂ holo-, 2♂ 3♀ paratypes, labelled: New Guinea, Terr. of Papua, New Hanover, 1954, J. H. Ardley, *Segestidea hanoverana* nov. sp. Det. C. Willemse, appropriate type-labels (holotype lacks left mid leg, BMNH; 1♂ 2♀ BMNH; 1♂ 1♀ CW).

Additional material (all New Ireland District): Feni Island Group, Anir Plantation, on *Cocos nucifera*, x.1959, G. S. Dunn (1♀ 1♀ CW); Tabar Group, Tatau Island, Teripax Plantation, defoliating coconuts, severe outbreak, 23.vii.1955, J. Szent-Ivany (2♂ 1♀ CW; 1♂ DASF); New Ireland Eastcoast, Metakabul Plantation, on coconuts, 21.viii.1955, J. Szent-Ivany (1♂ 1♀ CW) (all labelled *Segestidea hanoverana* Will. Det. C. Willemse); New Hanover, Umbukul, 15.iii.1971, resting on fronds of *Cocos nucifera*, B. Dionsil (2♀ DASF); Lihir Group, Masahet Island, 21.ix.1955, J. Szent-Ivany, on old coconut palm (1♂ DASF); Lihir Group, Mahur Island, 21.vii.1955, on young palm, J. Szent-Ivany (1♂ DASF); New Hanover, Baikep Village garden, 21.viii.1955, J. Szent-Ivany, on young

coconut palms (1 ♀ DASF); New Hanover, Tioputuk & Metevol, 11—15.iii.1971, B. Dionsil, resting on fronds of *Cocos nucifera* (1 ♀ DASF); New Hanover, 5.v.1932, coconuts (1 ♂ 1 ♀ BMNH).

Comparison of the types of *Sexava leefmansii*, *Segestidea hanoverana* and other material at hand reveals clearly that they are conspecific and should be arranged under *Segestidea*.

A general description can be found in the original ones of *leefmansii* and *hanoverana*. The species differs from the type-species as follows.

Slightly smaller (pl. 13 figs. 83, 84, pl. 14 fig. 85). Lower margin of pronotal lateral lobe from regularly to obtuse-angularly rounded, deepest point about in middle. Flexed wings reaching from distal end of proximal third to middle of hind tibia, in female to tip or just beyond tip of ovipositor. Fore wings long and wide, margins about parallel, in apical third hind margin more and fore margin less tapering towards widely rounded apex; archidictyon well-developed; transverse veins less numerous, in costal area irregular. Male stridulatory file (pl. 16 fig. 112) narrowly fusiform, slightly arcuate, 3.0—3.2 mm long, number of teeth 132—145 of which about 50—70 cover anterior third of file length. Width of file but very slightly and gradually increasing in anterior third of file length, reaching maximum of 0.3 mm near middle of file, from there slightly decreasing posteriorly. Spacing of teeth slightly and gradually increasing in anterior third, about regular over remaining of file length. Mirror (pl. 18 fig. 120) elongate-elliptical, about 3 mm long and 2 mm wide, fold moderately developed and inflated, its outline convex to slightly sinuate. Spines of legs as in type-species, ventral ones of hind femur hook-like as usual. Male cercus (pl. 15 fig. 104) much less incurved, near apex abruptly narrowing to short, strong, incurved tooth. Male subgenital plate (pl. 15 fig. 96) narrow, 6—7 times as long as smallest width, slightly widening apically, lateral margins slightly concave, margins of apical incision often crenulated. Ovipositor with upper margin straight or almost so, reaching from distal end of proximal third to middle of hind tibia.

General colour from pale to dark brown, seldom green. Antennae slightly annulated pale and dark brown. Head and thorax of general colour. Fore wing usually mottled with darker brown areas and dots, membrane infuscated. Legs of general colour, basal part of lower and inner side of hind femur solid black. Spines brown, tips black, tarsi from below dull dark brown.

Measurements: body ♂ 46—53, ♀ 51—59; fore wing ♂ 59—65, ♀ 72—75; hind femur ♂ 40—42, ♀ 41—45; ovipositor 30—34.

Distribution. As far as known, confined to the New Ireland District of the Bismarck Archipelago (map 3).

Localities: New Hanover (C. Willemse, 1957); Lawongai (C. Willemse, 1940); Namaoroso (C. Willemse, 1940); Tioputuk and Metevol; Umbukul; Baikop; New Ireland, Metakabul Plantation (F. Willemse, 1966); Feni Is., Anir Plantation (F. Willemse, 1966); Tabar Is., Tatau I., Teripax Plantation (F. Willemse, 1966); Lihir Group, Masahet I.; Mahur I.



Discussion. The species is well-defined by a number of characters. The coloration of the hind femur is a conspicuous feature. The male stridulatory file resembles that of *gracilis simulatrix*, but is shorter and narrower.

In the original description of *leefmansi*, the type-localities were recorded from the New Hebrides. Apparently this was a mis-interpretation for the abbreviation N.H. on the locality-label. Direct information given by Prof. Bühler, who collected the specimens (via Dr. Baroni-Urbani, in litt. 24.xi.1975) confirms that the specimens originate from New Hanover. As far as known, *Sexavae* do not occur in the New Hebrides.

The species lives together with *Segestidea gracilis gracilis*.

***Segestidea acuminata* (Kästner, 1934) comb. nov.**

(pl. 14 figs. 86, 87, map 3)

*Segestes acuminatus* Kästner, 1934: 50, figs. 18—19.

Material studied: ♀ holotype, labelled: Coll. Br. v.W. Milne Bay (Neu Guinea) Staud., *Segestes* sp. determ. Karny, 21.673, *Segestes acuminatus* Käst. ♀ A. Kästner det., Typus (NMW) (both antennae, right fore tibia, tarsi of four anterior legs, both cerci, tip of right middle tibia lacking and tips of both fore wings slightly damaged).

The holotype (pl. 14 figs. 86, 87) agrees fairly well with the original description except for two details. The intact left fore and mid tibiae bear a posterior dorso-apical spike, both apparently overlooked by Karny who studied the specimen, and by Kästner when describing his species. This character disagrees with *Segestes* and assigns the species to *Segestidea*. Further it can be seen that the apex of the fore wing, although slightly damaged, is truncated rather than narrowly rounded.

Other marked characters are the thorn-like fastigium of the vertex, which extends just beyond the scape. The pronotal dorsum is somewhat flattened in the middle, slightly rounded laterally, fore and hind margins each bearing two lateral and one median obtuse tubercles. Lower margin of pronotal lateral lobe obtuse-angularly rounded, deepest point just before the middle. The flexed wings reach the tip of the ovipositor, which reaches as far as the middle of the hind tibia. The venation of the fore wing agrees with that of the genus. Ovipositor is comparatively short and slightly upcurved. The subgenital plate is wider than long, slightly incised apically with widely rounded lobes. Fore and mid femora with 5—6 spines on the anteroventral margin. All knee-lobes with one spine. Fore and mid tibiae with 3 dorsal spines on the anterior margin, posterior margin of fore tibia unarmed, that of the mid tibia with 3 spines, dorso-apical spines not included. General colour is rusty brown. The apex of the fastigium of the vertex and a lateral stripe over the pronotal dorsum blackish. Fore wing with scattered dark brown points, caused by dark brown membrane between the archdictyon.

Measurements: body ♂ 38; fore wing 47; hind femur 28; ovipositor 20.

Distribution. Known only from the holotype, Papua: Milne Bay (map 3).

Discussion. The species is badly defined. It comes near *marmorata* (see below).

The distinction indicated in the key appears not reliable. Topotypic material, including the male, is needed to establish the differences between both taxa.

### ***Segestidea marmorata* I. Bolívar, 1903**

On account of similar considerations as given for *gracilis*, two subspecies in *marmorata* can be recognized: nominate *marmorata* and *marmorata occidentalis* ssp.n.

### ***Segestidea marmorata marmorata* I. Bolívar, 1903**

(pl. 15 figs. 97, 105, pl. 17 fig. 113, pl. 18 fig. 121, map 3)

*Segestidea marmorata* I. Bolívar, 1903: 167.

*Segestes acuminatus*; C. Willemse, 1961: 108, figs. 18, 19.

Material studied: E. New Guinea, Bubia, Markham Valley, 50 m, 19.ix.1955, J. L. Gressitt, *Segestes acuminatus* Kästner Det. C. Willemse 1960 (1 ♂ BPBM).

The species was described after a single female from: Sattelberg, Golfe Huon, Biró, 1898. Until now, no further material became available. Unfortunately the holotype has been lost (TMA) (Steinmann, in litt. 3.xii.1975) and other material could not be traced (IEM; V. Llorente, in litt. 9.i.1976). The male before me agrees fairly well with Bolívar's description and its locality is not far from the type-locality. Preliminarily, the specimen is assigned to nominate *marmorata*. It differs from the type-species as follows.

#### **Redescription.**

♂ smaller, more slender (C. Willemse, 1961: fig. 19). Fastigium of vertex (C. Willemse, 1961: fig. 18) thorn-like, apex acute, slightly upcurved, extending far beyond the antennal scrobae, reaching apical margin of scape. Pronotal dorsum somewhat flattened medially, slightly rounded laterally, anterior margin almost, posterior margin quite straight, both margins with weak median tubercle. Pronotal lateral lobe about as long as high, lower margin obtusely angulate, deepest point about in the middle.

Flexed wings reaching just beyond middle of hind tibia. Fore wing long and narrow, margins about parallel, very slightly narrowing towards wide, obliquely truncated and slightly emarginate apex; archidictyon well-developed; transverse veins not incrassate, ill-defined and but few in number. Stridulatory file of the male at hand (pl. 17 fig. 113) partly torn off from the membrane, fusiform, slightly arcuate, 2.9 mm long, number of teeth 105 of which anterior 30 fine and about blunt, covering anterior seventh of file length, remaining 75 teeth sharp. Width of file strongly increasing in anterior part, reaching maximum 0.4 mm in middle of file, decreasing posteriorly. Spacing of teeth very narrow in anterior part, strongly increasing towards middle of file, from there about regular and scarcely decreasing posteriorly. Mirror (pl. 18 fig. 121) roughly trapezoid, about 3 mm long and 2 mm wide, fold extending well over mirror with strongly inflated basal half,

its outline convex basally, running obliquely towards postero-apical angle of mirror.

Fore and mid femora with 3 spines on apical half of anteroventral margin. All knee-lobes with one spine. Fore tibia with 3 and 6, mid tibia with 2 and 3 dorsal spines on posterior and anterior margins, respectively, dorso-apical spines not included. Spines of hind femur hook-like. Cercus (pl. 15 fig. 105) slender, incurved and slightly tapering apically. Subgenital plate (pl. 15 fig. 97) small, narrow, about four times as long as smallest width, apex divided by V-shaped incision into pair of narrow lobes, styli present.

General coloration mottled pale and dark brown. Fastigium of vertex from above, pronotal dorsum and cubito-anal areas of fore wing, dark brown. Antennae slightly annulated. Fore wing distinctly mottled pale and dark brown, combined with smaller and larger areas of transparent membrane; hind margin narrowly bordered yellowish white in proximal half. Inner side of hind femur castaneous brown. Spines of legs black, dorsal spines of hind tibia brown, tips black.

♀, after Bolívar: Lamina subgenitalis postice rotundata, medio obtuse angulato-emarginata. Ovipositor subrectus, pallidus, apice magis infuscatus.

Measurements (♀ after Bolívar): body ♂ 46, ♀ 45; fore wing ♂ 59, ♀ 59; hind femur ♂ 31, ♀ 33; ovipositor 24.

Distribution. Known only from East New Guinea: Morobe District (map 3).

Localities: Sattelberg (Bolívar, 1903); Bubia.

Discussion. The nominate subspecies is well-defined, although variation is insufficiently known. It links *Segestidea* with *Segestes*, which is apparent when comparing *marmorata* with *Segestes stibicki*, *brevipennis* and *cornelii*. As pointed out under *acuminata*, that species might be synonymous with nominate *marmorata*.

### ***Segestidea marmorata occidentalis* subsp. nov.**

(pl. 14 figs. 88—90, pl. 15 figs. 98, 106, pl. 17 fig. 114, pl. 18 fig. 122, map 3)

Material studied. ♂ holotype, labelled: Neth. New Guinea, Dojo, iv.1958, G. den Hoedt (CW); paratypes: Hollandia, Ned. Nieuw Guinea Exp. 1911 Dr. P. N. v. Kampen (2♂ 2♀ RNH) (holotype lacks both antennae and part of some tarsi, paratypes discoloured and more damaged).

#### **Description.**

♂ (pl. 14 figs. 88, 89). Differs from nominate subspecies in larger number of teeth of male stridulatory file (pl. 17 fig. 114). The latter of similar length, 2.9—3.1 mm, number of teeth about twice as large, 198—203, maximum width of file slightly smaller, 0.3 mm, spacing of teeth twice as narrow. Mirror (pl. 18 fig. 122) of right male fore wing, abdominal terminalia (pl. 15 figs. 98, 106) and coloration about as in nominate subspecies.

♀ (pl. 14 fig. 90). Flexed wings reach middle of hind tibia, extending beyond tip of ovipositor. Ovipositor short, slightly upcurved, reaching about distal end of proximal third of hind tibia. General coloration more uniform.

Measurements: body ♂ 39—47, ♀ 36—40; fore wing ♂ 56—57, ♀ 51—52; hind femur ♂ 31—33, ♀ 30—31; ovipositor 20—21.

Distribution. Known only from the type-series, West New Guinea: Hollandia and nearby Dojo (map 3).

Discussion. More material is needed to establish precisely the distinction between *occidentalis* and nominate *marmorata*. Although the number of teeth of the male stridulatory file in *Sexava coriacea* varies in a similar degree, that number is defined by the length of the file, while the spacing of the teeth is about similar. This is not the case in the *marmorata* material, which justifies the subspecific distinction between the nominate form and *occidentalis*.

No previous records.

### ***Segestidea soror* Hebard, 1922**

*Segestidea soror* Hebard, 1922: 178, pl. 16 figs. 3, 4.

Known only from the typical pair (ANSP).

Distribution. The Moluccas: Obi (Hebard, 1922).

Discussion. I have before me a male with the tip of abdomen badly damaged. It is labelled: Dodinga, Halmahera, Bernstein (CW). As far as can be judged, the specimen agrees with Hebard's species. Especially the shape of the fore wing with obliquely truncated apex fits *soror* perfectly. The stridulatory file is 3.9 mm long, slightly arcuated and fusiform, number of teeth 79 of which the anterior 28 fine and less sharp than the remaining 51 ones. Width of the file reaching maximum of 0.47 mm in anterior fourth of file length, decreasing posteriorly to about a third of the maximum width. Spacing of the teeth very fine and increasing in anterior third, decreasing posteriorly to about half widest spacing. Mirror twice as long as wide, elliptical; fold extending well over the mirror, outline almost straight and parallel to the hind margin of the wing.

### ***Segestidea punctipennis* I. Bolívar, 1903**

*Segestidea punctipennis* I. Bolívar, 1903: 168.

Known only from the ♀ holotype (IEM).

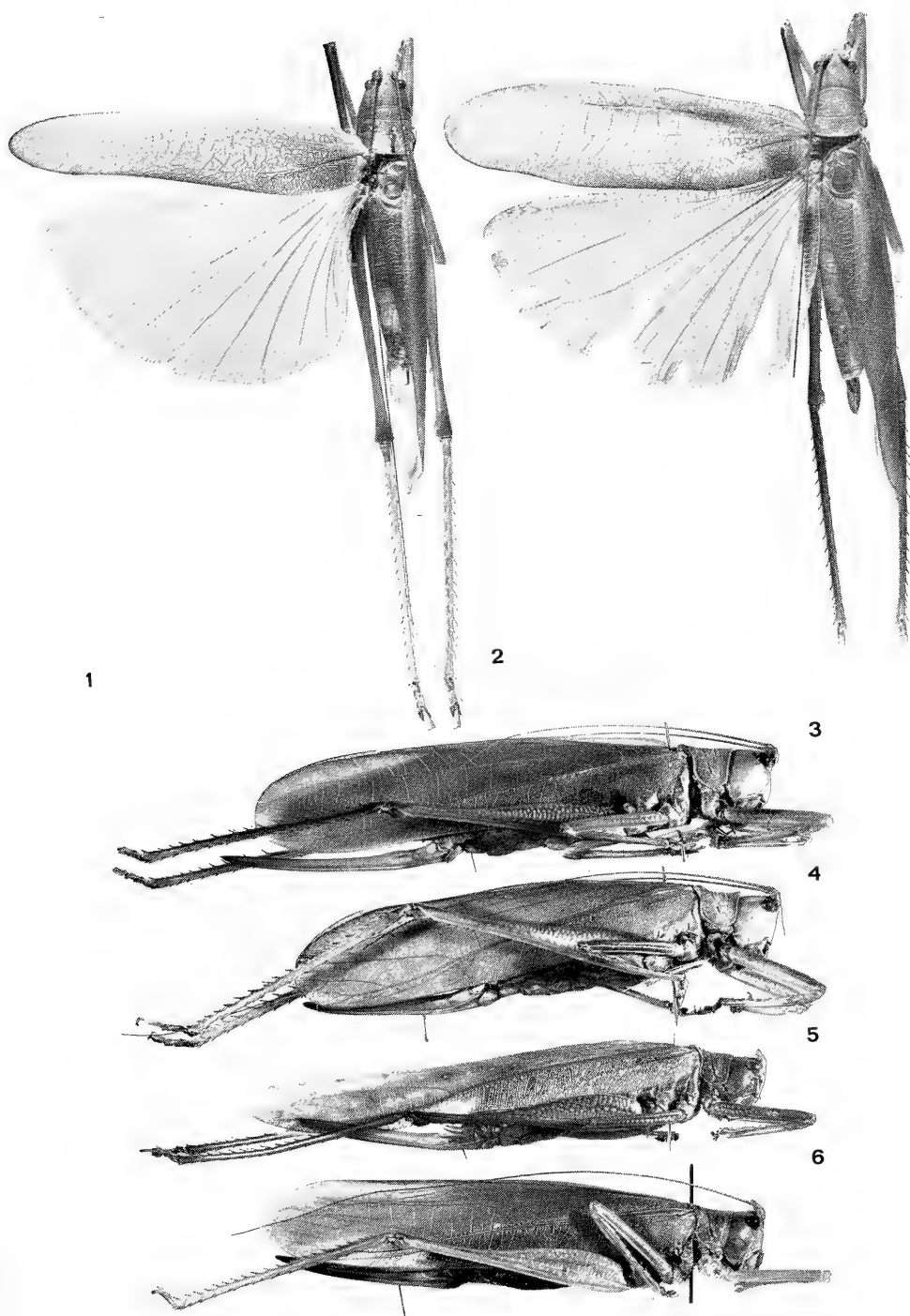
Distribution. The Philippine Is.: Irocin, Albay (Bolívar, 1903).

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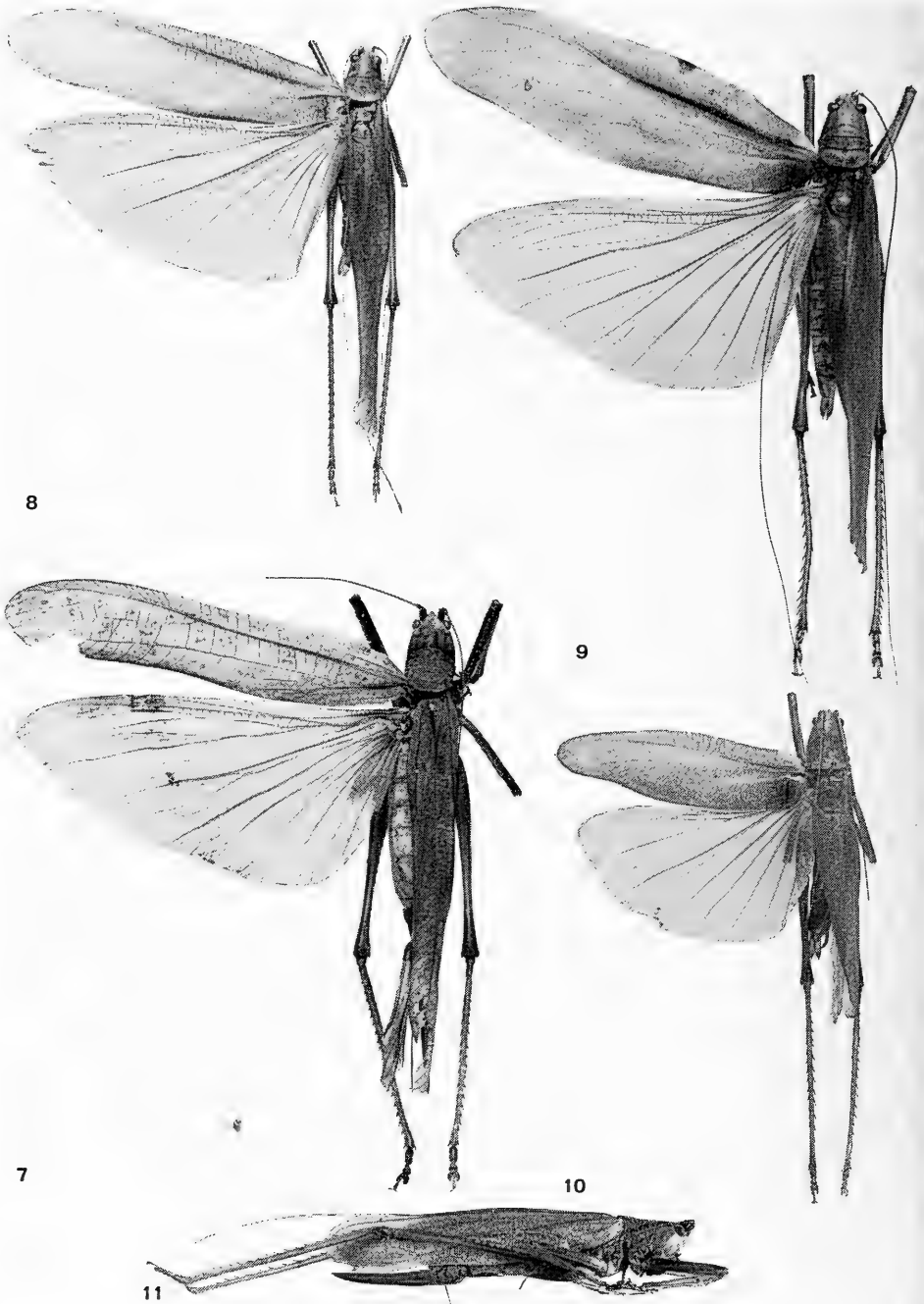
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Figs. 1—4. *Sexava coriacea* (L.): 1, ♂ (Ambon, CW); 2, ♂ (Obi, CW); 3, ♀ (Obi, paratype *S. grandis*, CW); 4, ♀ (Sangihe I., ITZ). Figs. 5—6. *S. nubila* (Stål): 5, ♀ (Sorong, CW); 6, ♀ (Talaud Is., BMNH).

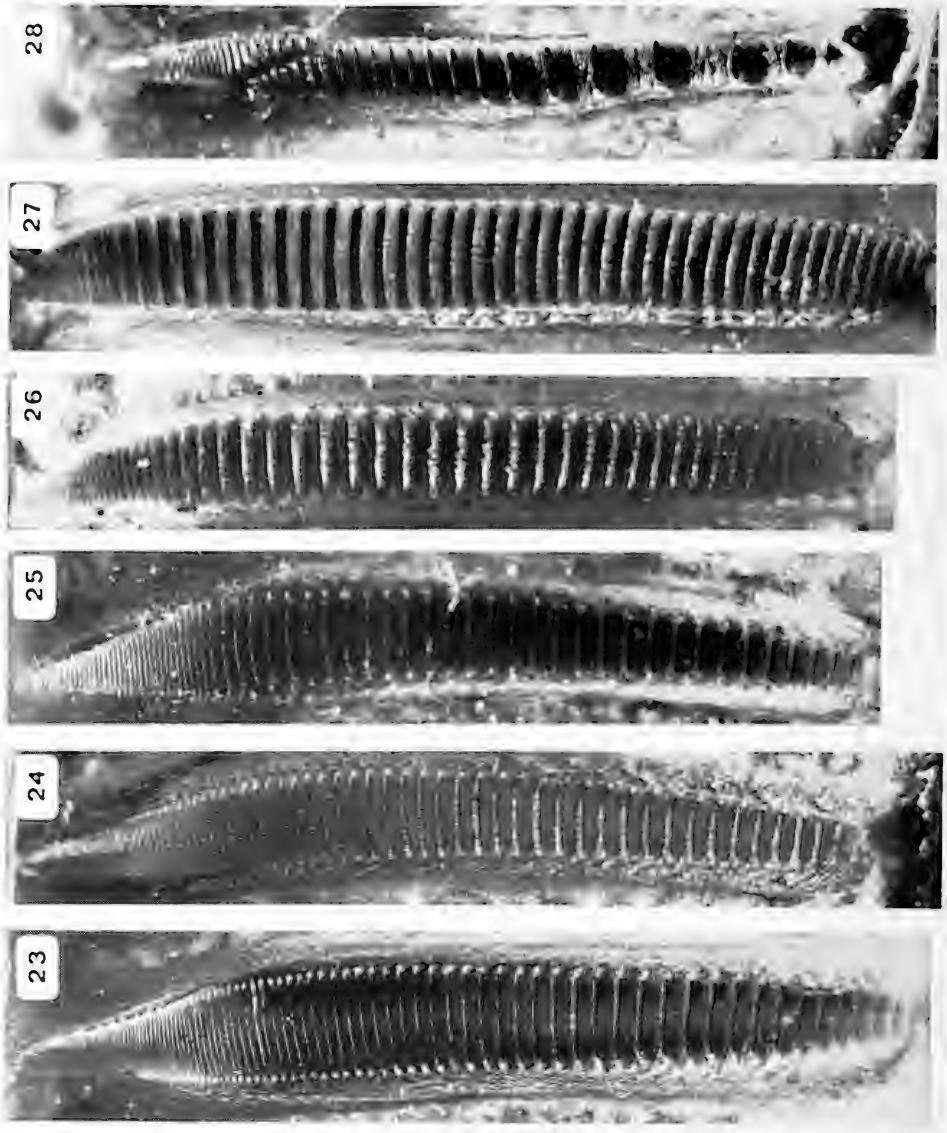


Figs. 7—9. *Sexava nubila* (Stål): 7, ♀ (holotype); 8, ♂ (Mindiptana, CW); 9, ♂ (Beo, Talaud Is., RNH).  
Figs. 10—11. *S. karnyi* Leefmans: 10, ♂ (Ampana, ITZ); 11, ♀ (Posso, ITZ).





Figs. 12—22. *Sexava* species: 12—17, male subgenital plate: 12—14, *coriacea* (L.) (12, Obi, CW; 13, Ambon, RNH; 14, Halmaheira, CW); 15—16, *nubila* (Stål) (15, Sorong, CW; 16, Talaud Is., ITZ); 17, *karnyi* Leefmans (Ampana, ITZ); 18—22, male cercus: 18—19, *coriacea* (L.) (18, Ambon, RNH; 19, Sangihe Is., BMNH); 20—21, *nubila* (Stål) (20, Mindiptana, CW; 21, Talaud Is., ITZ); 22, *karnyi* Leefmans (Ampana, ITZ).



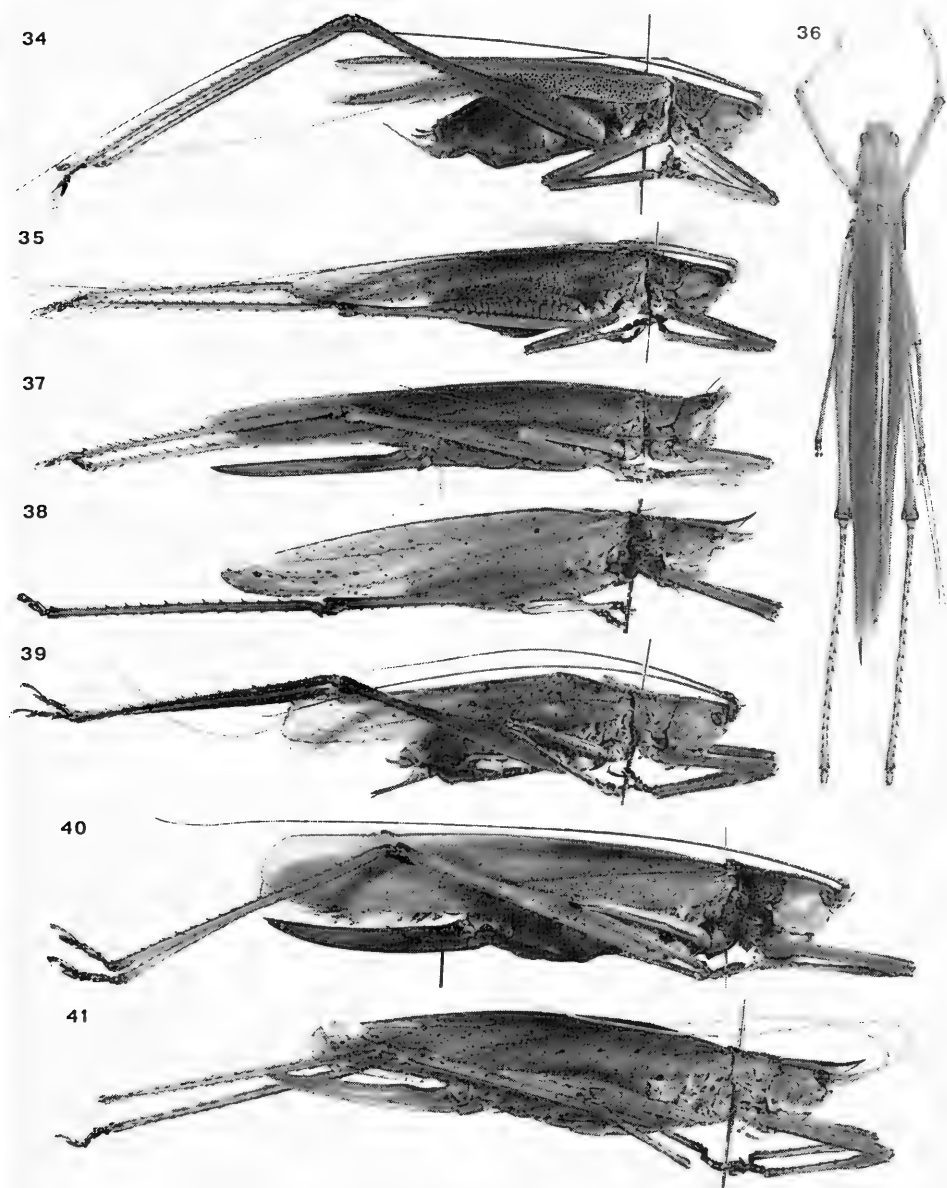
Figs. 23—28. *Sexava* species, male stridulatory file; 23—25, *coriacea* (L.) (23, Obi, CW; 24, Halmaheira, CW; 25, Ambon, RNH); 26—27, *nubila* (Stål) (26, Koor, CW; 27, Talaud Is., ITZ); 28, *karnyi* Leefmans (Ampana, ITZ).



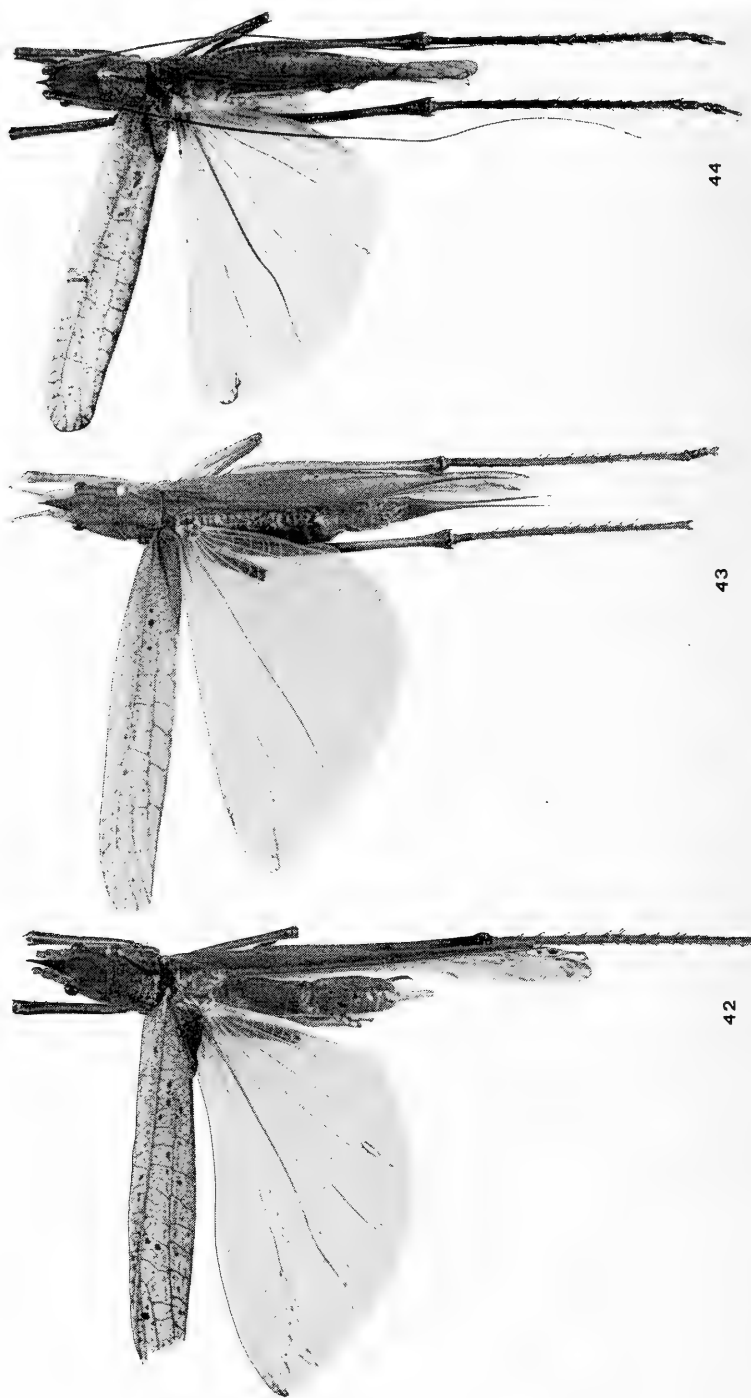
Fig. 29. *Sexava coriacea* (L.), stridulatory area of right male fore wing (Obi, CW).



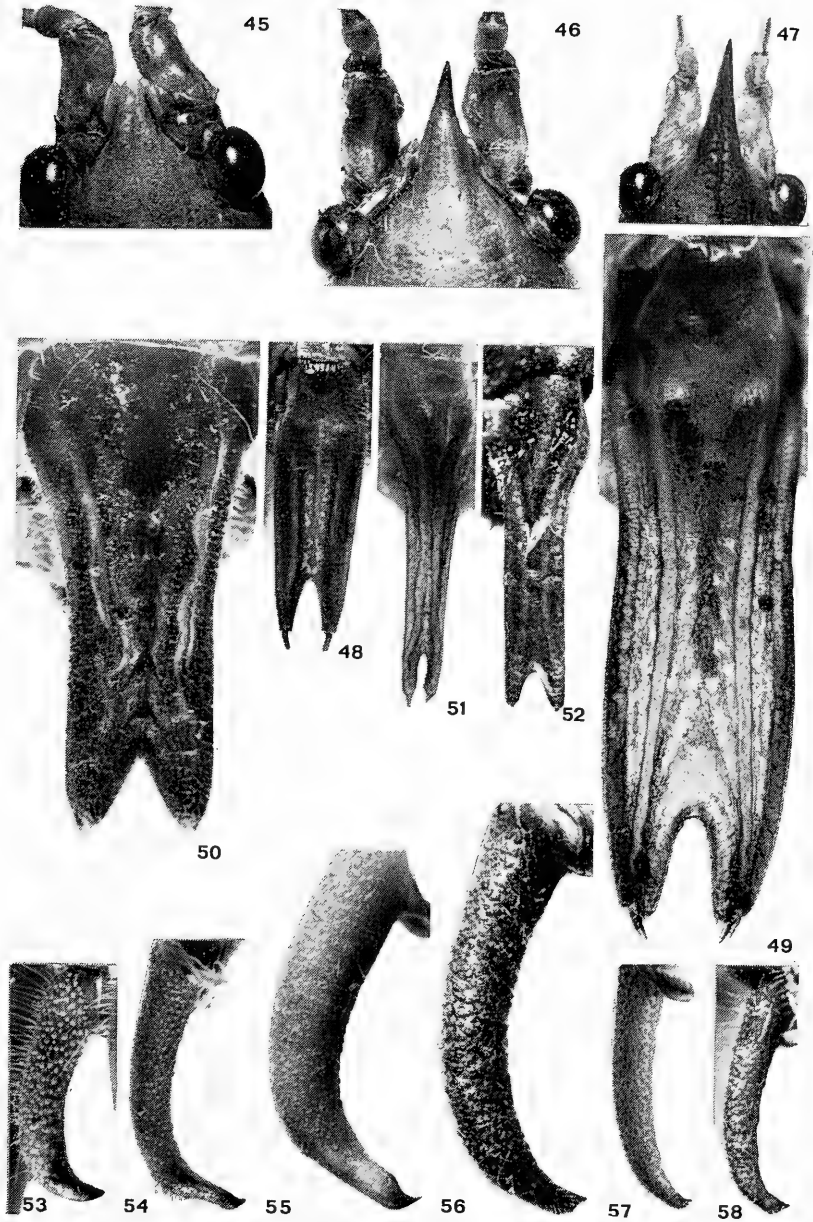
Figs. 30—33. *Segestes* species: 30, *vittaticeps* Stål (♂ lectotype); 31, *cornelii* sp.n. (♂ holotype); 32, *unicolor* Redtenbacher (♂ Koror, Palau, CAS); 33, *decoratus* Redtenbacher (♂ Bubia, CW).



Figs. 34—41. *Segestes* species: 34, *vittaticeps* Stål (♂ lectotype); 35, *unicolor* Redtenbacher (♂ Koror, Palau, CAS); 36—37, *decoratus* Redtenbacher (36, ♀ holotype; 37, ♀ Murua Agr. Stat., DASF); 38, 41, *stibicki* sp.n. (38, ♂ paratype; 41, ♀ paratype); 39, *brevipennis* sp.n. (♂ holotype); 40, *cornelii* sp.n. (♀ paratype).

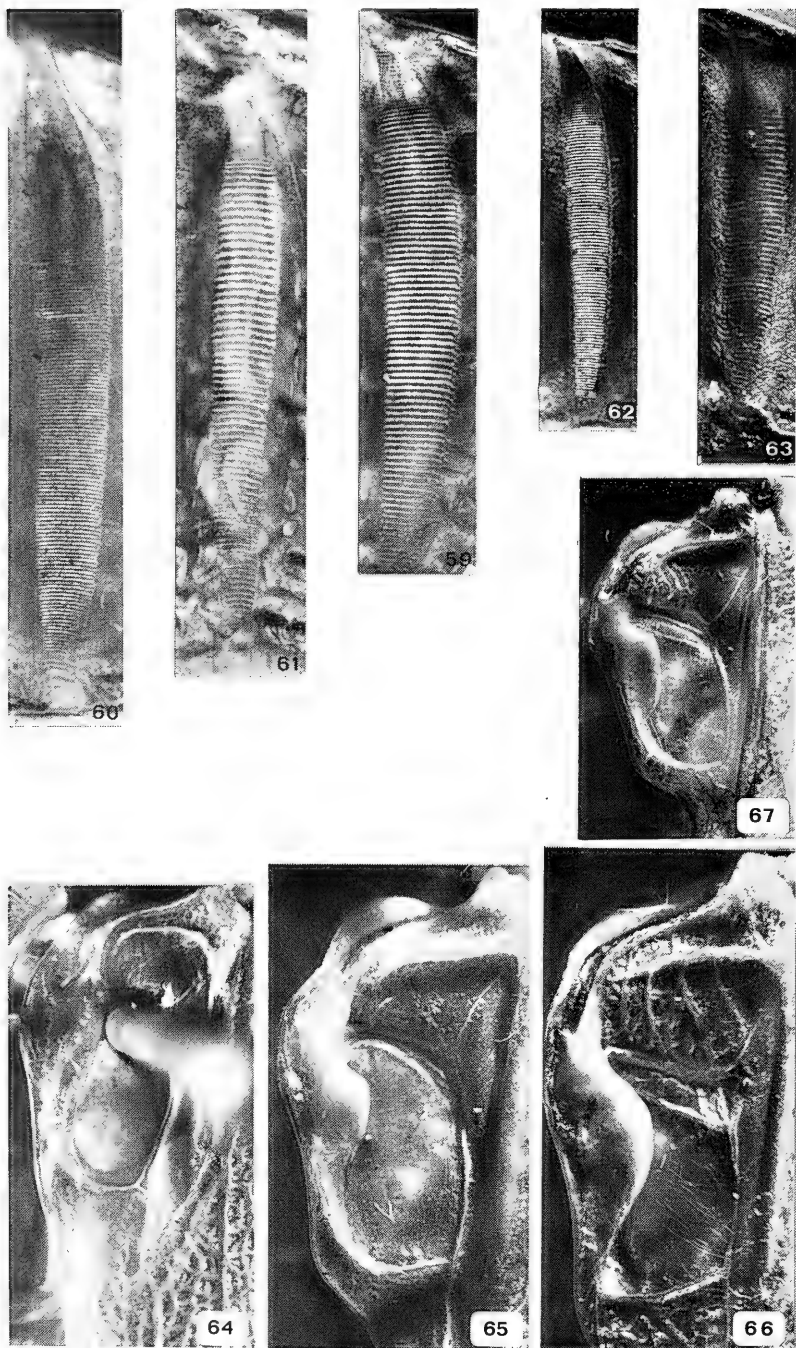


Figs. 42—44. *Segestes* species: 42—43, *stibicki* sp.n. (42, ♂ holotype; 43, ♀ paratype); 44, *brevipennis* sp.n. (♂ holotype).



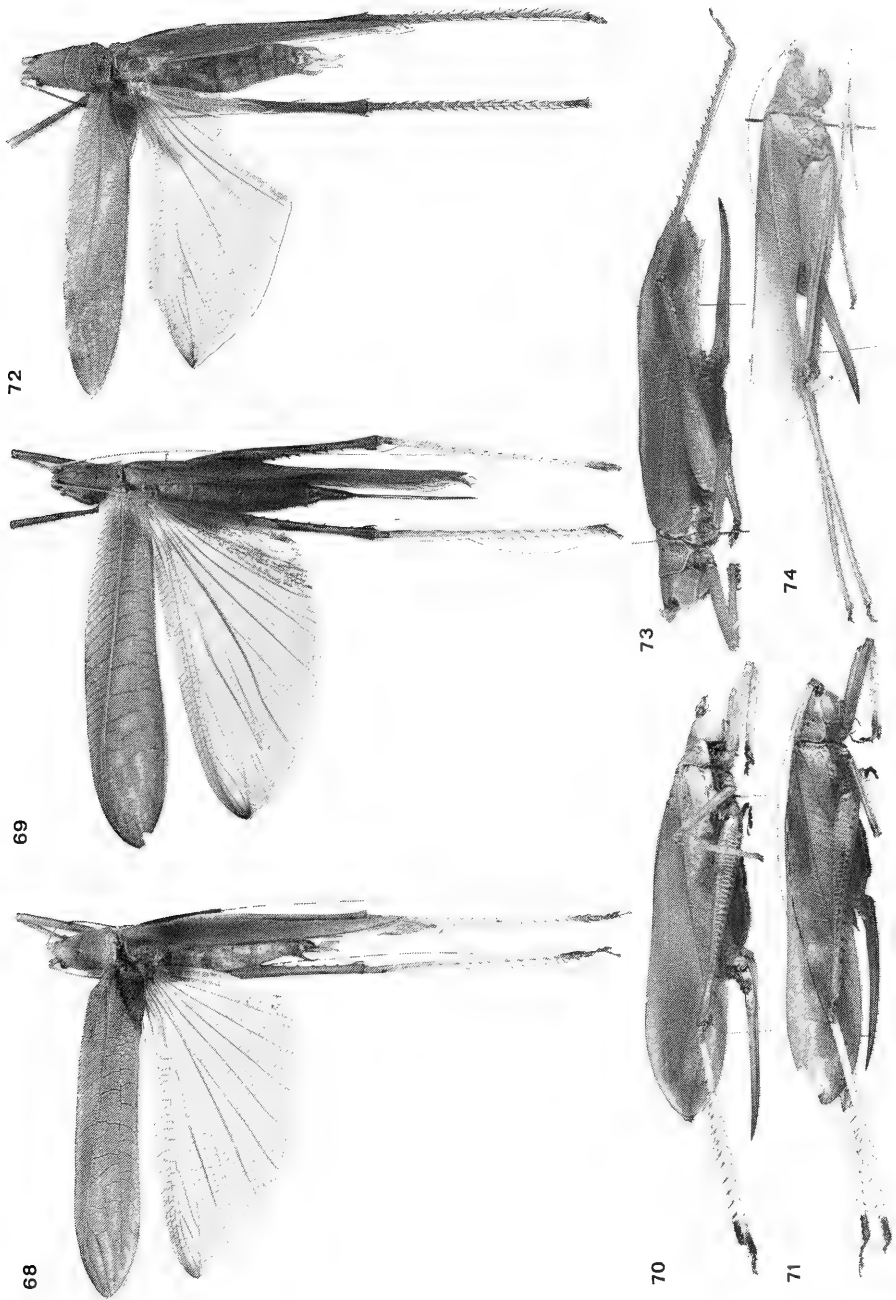
Figs. 45—58. *Segestes* species: 45—47, fastigium of vertex: 45, *decoratus* Redtenbacher (♂ Casey's Pl., Popondetta, DASF); 46, *cornelii* sp.n. (♂ paratype); 47, *stibicki* sp.n. (♀ paratype); 48—52, male subgenital plate: 48, *vittaceps* Stål (lectotype); 49, *decoratus* Redtenbacher (Siki, DASF); 50, *cornelii* sp.n. (paratype); 51, *stibicki* sp.n. (holotype); 52, *brevipennis* sp.n. (holotype); 53—58, male cercus: 53, *vittaceps* Stål (lectotype); 54, *unicolor* Redtenbacher (Koror, Palau, CAS); 55, *decoratus* Redtenbacher (Siki, DASF); 56, *cornelii* sp.n. (paratype); 57, *stibicki* sp.n. (holotype); 58, *brevipennis* sp.n. (holotype).



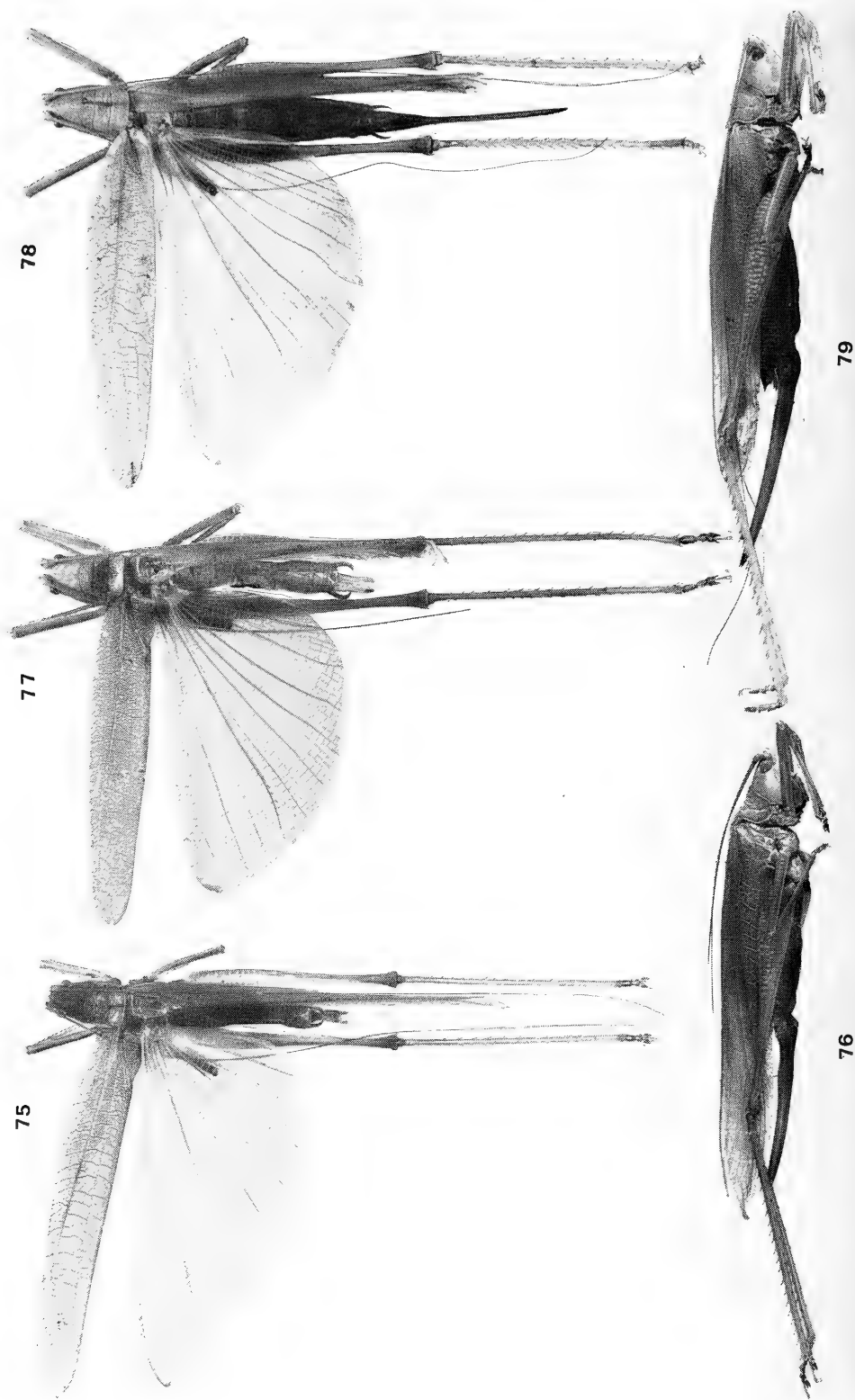


Figs. 59—67. *Segestes* species: 59—63, stridulatory file of left male fore wing: 59, *unicolor* Redtenbacher (Koror, Palau, CAS); 60, *decoratus* Redtenbacher (Siki, DASF); 61, *cornelii* sp.n. (paratype); 62, *stibicki* sp.n. (holotype); 63, *brevipennis* sp.n. (holotype). 64—67, stridulatory area of right male fore wing: 64, *vittaticeps* Stål (lectotype); 65, *decoratus* Redtenbacher (Casey's Pl., Popondetta, DASF); 66, *cornelii* sp.n. (paratype); 67, *stibicki* sp.n. (holotype).

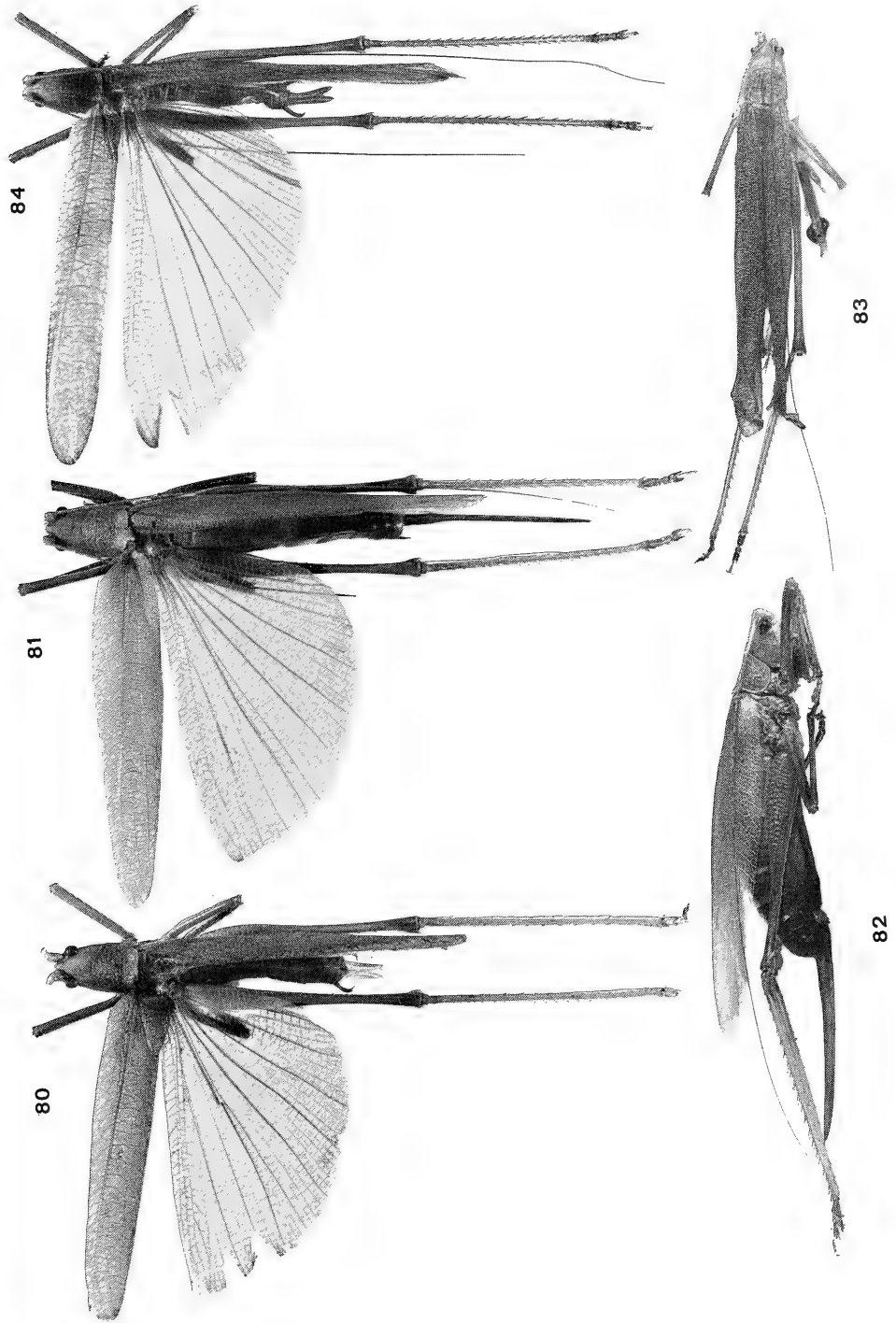




Figs. 68—74. *Segestidea* species: 68—71, *novaeguineae* (Brancsik) (68, ♂ Kulili Pl., Karkar I., DASf; 69, ♀ holotype of *Sexava femorata*; 70, ♀ Hollandia, RNH; 71, ♀ Port Moresby, CW); 72—73, *rufipalpis* (C. Willemse) (72, ♂ holo-, 73, ♀ allotype); 74, *uniformis* (C. Willemse) (♀ holotype).



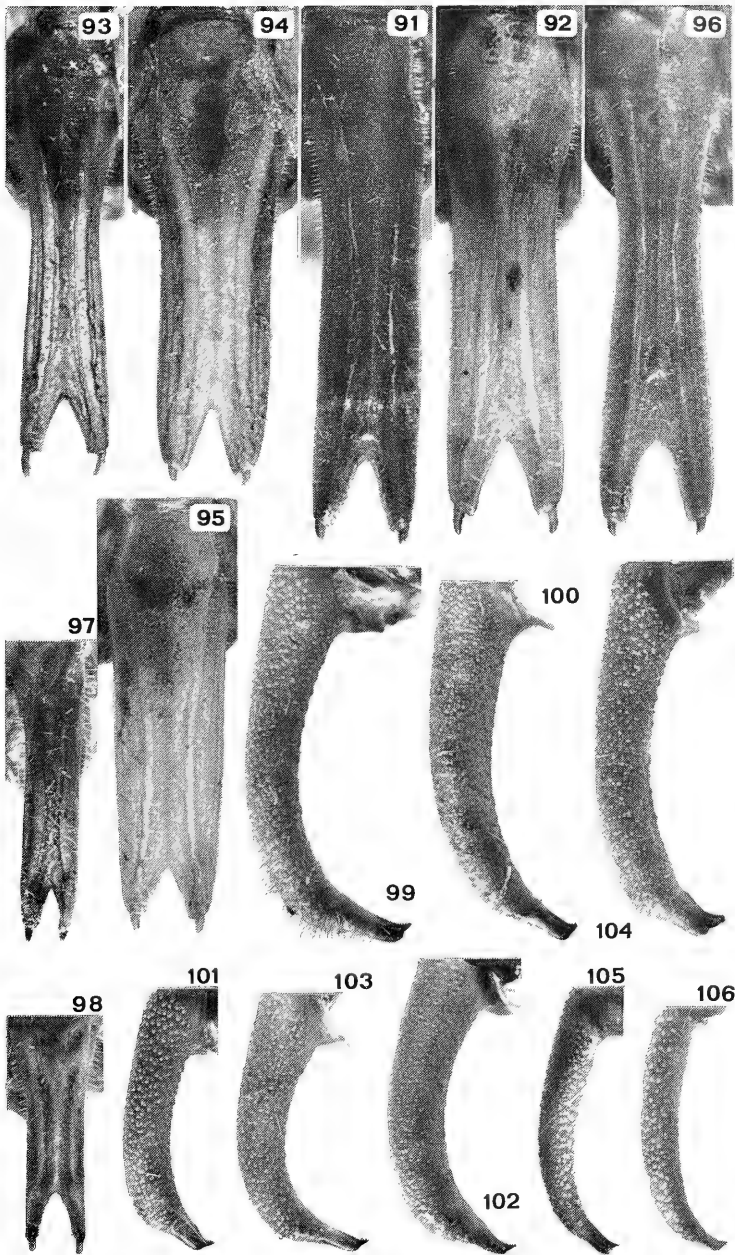
Figs. 75—79. *Segestidea* species: 75—76, *uniformis* (C. Willemse) (75, ♂ Tulo Pl., Manus I., DASF; 76, ♀ Pak I., DASF); 77—79, *gracilis gracilis* (C. Willemse) (77, ♂ Londolovit, Lihir Is., CW; 78, ♀ Mahur I., CW; 79, idem).



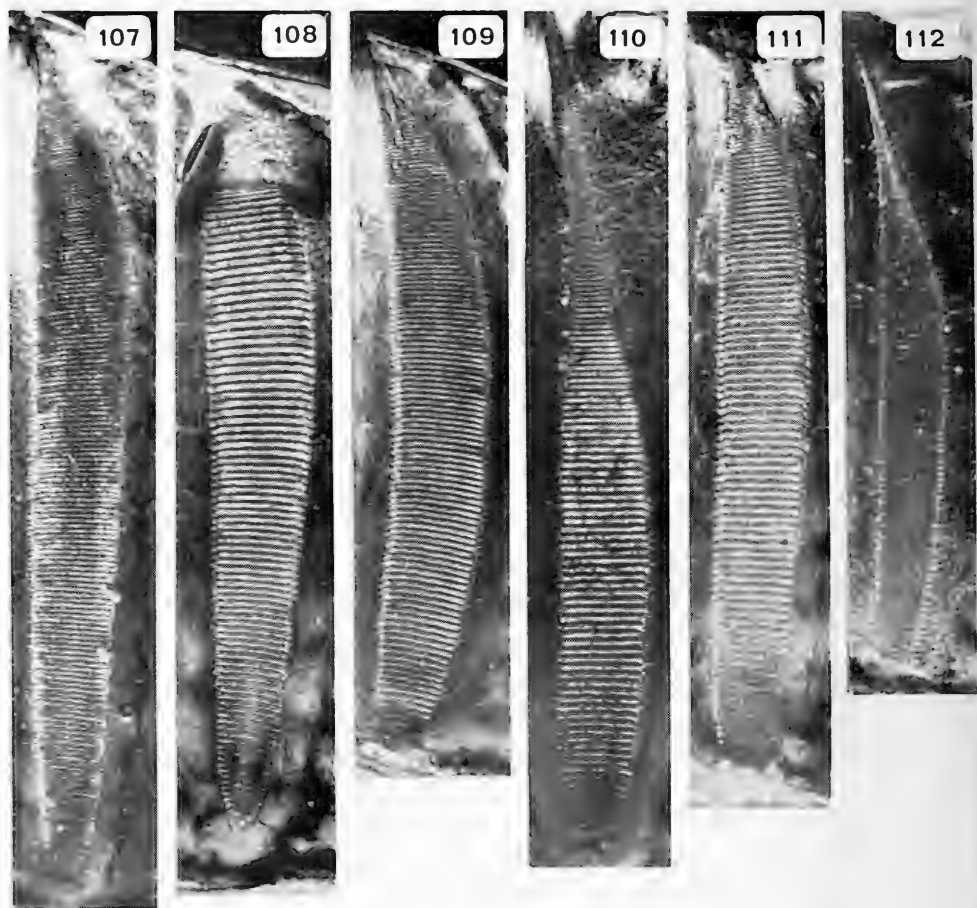
Figs. 80—84. *Segestidea* species: 80—82, *gracilis simulatrix* ssp.n. (80, ♂ holo-, 81, ♀ paratype, similar locality, CW; 82, idem); 83—84, *leefmansi* (C. Willemse) (83, ♂ holotype; 84, ♂ Metakabul Pl., New Ireland, CW).



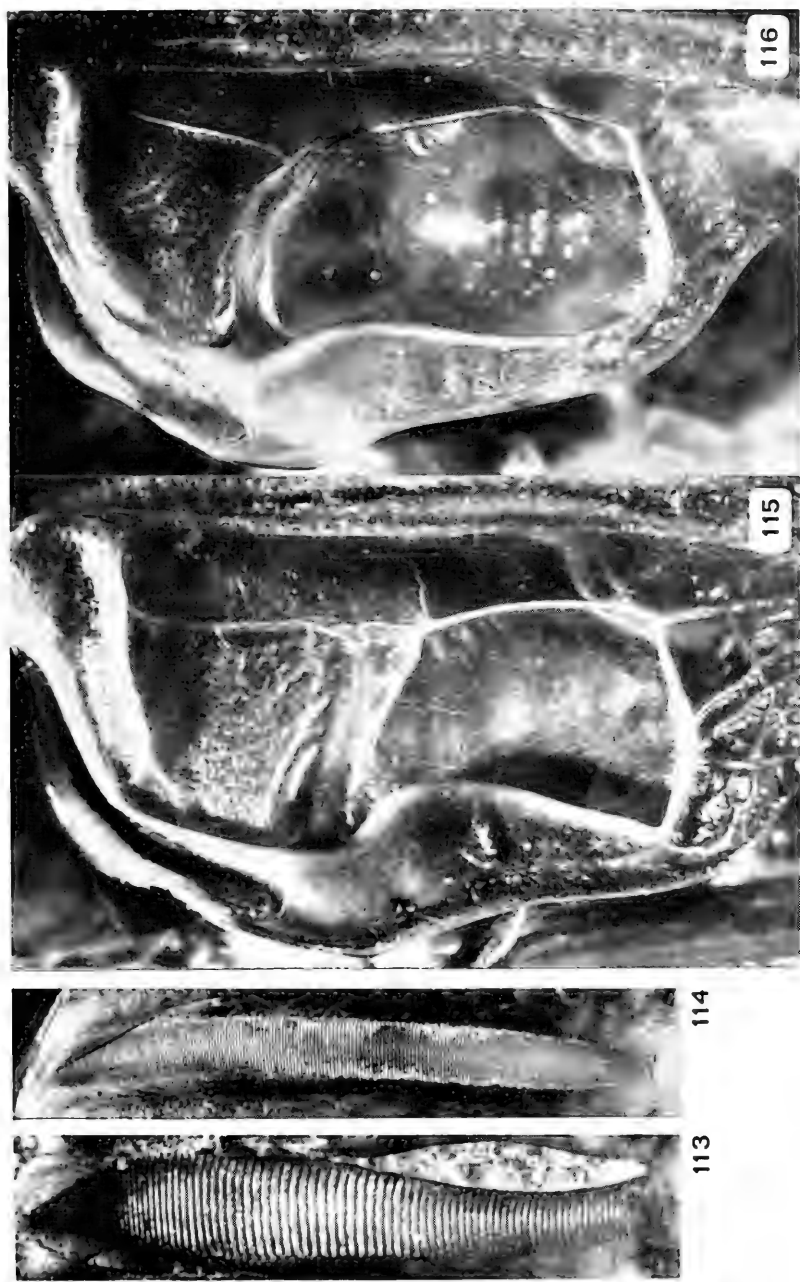
Figs. 85—90. *Segestidea* species: 85, *leefmansi* (C. Willemse) (♀ Umbukul, New Hanover, DASF); 86—87, *acuminata* (Kästner) (♀ holotype); 88—90, *marmorata occidentalis* ssp.n. (88—89, ♂ holo-, 90, ♀ paratype, Hollandia).



Figs. 91—106, *Segestidea* species: 91—98, male subgenital plate: 91, *novaeguineae* (Brancsik) (Baliau Village, CW); 92, *rufipalpis* (C. Willemse) (paratype); 93, *uniformis* (C. Willemse) (Bundalis R. C. Mission, DASF); 94, *gracilis gracilis* (C. Willemse) (Masahet I., Lihir Is., CW); 95, *gracilis simulatrix* ssp.n. (Bainings St. Paul's, BPBM); 96, *leefmansi* (C. Willemse) (Teripax Pl., Tatau I., CW); 97, *marmorata marmorata* Bolívar (Bubia, BPBM); 98, *marmorata occidentalis* ssp.n. (holotype); 99—106, male cercus: 99, *novaeguineae* (Brancsik) (Bubia, CW); 100, *rufipalpis* (C. Willemse) (paratype); 101, *uniformis* (C. Willemse) (Bundalis R. C. Mission, Manus I., DASF); 102, *gracilis gracilis* (C. Willemse) (Masahet I., CW); 103, *gracilis simulatrix* ssp.n. (Bainings St. Paul's, BPBM); 104, *leefmansi* (C. Willemse) (Teripax Pl., Tatau I., CW); 105, *marmorata marmorata* Bolívar (Bubia, BPBM); 106, *marmorata occidentalis* ssp.n. (holotype).



Figs. 107—112. *Segestidea* species, stridulatory file of left male for wing: 107, *novaequinae* (Brancsik) (Kulili pl., Karkar I., DASF); 108, *rufipalpis* (C. Willemse) (paratype); 109, *uniformis* (C. Willemse) (Bundalis R. C. Mission, Manus I., DASF); 110, *gracilis gracilis* (C. Willemse) (Masahet I., CW); 111, *gracilis simulatrix* ssp.n. (Bainings St. Paul's, BPBM); 112, *leefmansi* (C. Willemse) (Masahet I., DASF).



Figs. 113—116. *Segestidea* species: 113—114, stridulatory file of left male fore wing; 113, *marmorata marmorata* Bolivar (Bubia, BPBM); 114, *marmorata occidentalis* ssp.n. (holotype); 115—116, stridulatory area of right male fore wing; 115, *novaeguineae* (Brancsik) (Kulili Pl., Karkar I., DASF); 116, *rufipalpis* (C. Willemse) (paratype).





Figs. 117—122. *Segestidea* species, stridulatory area of right male fore wing; 117, *uniformis* (C. Willemse) (Bundalis R. C. Mission, Manus I., DASF); 118, *gracilis gracilis* (C. Willemse) (Matakan Pl., DASF); 119, *gracilis simulatrix* ssp.n. (Bainings St. Paul's, BPBM); 120, *leefmansi* (C. Willemse) (Masahet I., DASF); 121, *marmorata marmorata* Bolivar (Bubia, BPBM); 122, *marmorata occidentalis* ssp.n. (holotype).



## INDEX

(Synonyms in italics)

acuminata	253
beieri	229
brevipennis	236
celebensis	229
coriacea	220
cornelii	237
decoratus	231
<i>Eumossula</i>	238
<i>femorata</i>	242
frater	229
fuscus	229
gracilis	248
gracilis gracilis	248
gracilis simulatrix	250
<i>grandis</i>	220
<i>hanoverana</i>	251
insulana	246
karnyi	226
<i>lanceolata</i>	220
leefmansi	251
marmorata	254
marmorata marmorata	254
marmorata occidentalis	255
<i>Moristus</i>	218
novaequineae	242
nubila	222
<i>princeps</i>	242
punctipennis	256
punctipes	229
rufipalpis	245
Segestes	227
Segestidea	240
Sexava	218
soror	256
stibicki	235
unicolor	230
uniformis	246
vittaticeps	227



## REGISTER VAN DEEL 120

\* Een sterretje duidt aan een naam nieuw voor de wetenschap

\* An asterisk denotes a name new to science

## ARANEAE

alacris 1, 3  
arctica 18  
arcuata 30, 31  
arcuatus 30  
aspromontis 17, 18, 20  
Bathyphantes 25  
borealis 24  
camschaticus 7, 38, 45, 47,  
[48]

concinna 8  
concinnella 8  
cracens 42  
cristatus 3, 5, 6, 24, 40, 47  
\* drenskyi 6, 22, 47, 48  
expunctus 3  
faltonensis 17, 20  
flavipes 6, 8, 10, 12, 14, 42,  
[47]

\* floriana 6, 8, 28, 47, 48  
foliatus 41  
gallicus 8, 10  
henricae 12, 14  
herbicola 6, 7, 16, 42, 47  
jacksoni 6, 7, 32, 45, 47, 48  
\* jacksonoides 6, 7, 33, 34,  
[45, 47, 48]

leprosus 3, 5, 46  
Lepthyphantes 1 et seq.  
Linyphia 8, 12, 15, 17, 36  
mengei 6, 8-11, 12, 14, 42, 47  
minutus 3  
mughi 3  
nigriventer 36, 39  
nigriventris 6, 7, 36, 39, 45,  
[48]

pallidiventris 40  
pallidus 40  
\* perseus 5, 11, 47, 49  
pullatus 13  
pygmaea 15  
pygmaeus 25

sanfilippoi 18  
spiniger 6, 8, 27, 47, 48  
suldalensis 42  
taczanowskii 19, nota  
tarzanowskii 19, nota  
tenebricola 6, 7, 8, 12, 13, 30,  
[32, 46, 48]  
tenebricoloides 6, 7, 21, 48,  
[49]  
tenoides 42  
tenuis 6, 7, 14, 17, 42, 47, 48,  
[49]

Theridium 12  
tomskica 8  
trucidans 19  
zebra 42  
zebrinus 15, nota  
zelatus 42  
zibus 42  
zimmermanni 6, 8, 12, 14, 15,  
[18, 20, 23, 25, 26, 28, 41,  
45, 47, 48, 49]

## COLEOPTERA

\* addendum 83, 87  
\* bicornutum 83, 89  
Bolboceras 81  
Bolbogonium 77 sqq  
\* howdeni 87, 97  
impressum 82, 92  
\* insidiosum 83, 95  
\* pseudopunctatissimum 82,  
[90]

punctatissimum 87, 96  
\* scurra 83, 94  
triangulum 81, 83, 91  
\* wiebesi 83, 99

## DIPTERA

betulae 153, 154, 164, 165,  
[166, 167, 179, 180, 181]

\* brevipalpis 164, 165, 166,  
[167, 169, 177, 180, 181]  
Cecidomyia 153  
Clinodiplosis 154  
Hormomyia 153  
Aligotrophus 153  
Semudobia 153 sqq  
\* skuhravae 164, 165, 166,  
[174, 179, 180, 181]  
\* steenisi 164, 165, 166, 167,  
[170, 177, 180, 181]  
\* tarda 164, 166, 172, 179,  
[180, 181]

## HETEROPTERA

argentatus 199, 200, 206  
Gerris 199 sqq  
gibbifer 209, 210  
lacustris 199, 208, 210, 212  
najas 200  
odontogaster 199, 200, 205,  
[211]  
rufoscutellatus 210  
thoracicus 199, 200, 207, 210

## HYMENOPTERA

Arischnogaster 60  
Belonogaster 58  
binodis 58  
Calligaster 57 nota 3, 58  
cilipennis 63, 64  
cinerascens 57  
concinna 58  
cristatus 57  
cyanopterus 58  
Discoelius 57 nota 3  
drewseni 63, 64, 69  
Eustenogaster 60  
fuscus 58  
\* gracilipes 73

\* *Holischnogaster* 60, 70  
*Ischnogaster* 55, 56  
*Ischnogasteroides* 56  
*Liostenogaster* 57, 59  
 \* *Metischnogaster* 59, 60  
*miniatus* 58  
*montezuma* 58  
*Parischnogaster* 58, 60  
*Plagiolabra* 57  
*prominens* 58  
*spinipes* 57  
*Stenogaster* 55, 58, 59  
*strigosus* 58  
*williamsi* 58  
*Zethus* 57, 58

## ORTHOPTERA

*acuminatus* 240, 241, 253  
*ssp. annulata* (C.  
     [*kuekenthali*]) 146  
*beieri* 229  
*bimaculata* 137  
*brevipennis* 231, 236  
*caprai* 127, 138  
*carnipes* 109, 110, 112  
*celebensis* 229  
*Chitaura* 136  
*ssp. coerulipes* (C. *patagiata*)  
     [127  
*ssp. coerulipes* (C. *pervittata*)  
     [130, 132  
*coriacea* 219, 220  
*cornelii* 231, 237  
*Cranae* 110, 121 sqq  
*Cranaella* 109 sqq, 127  
*decoratus* 231  
*emendata* 150  
*Eumossula* 240  
*femorata* 211, 240, 242  
*fuscus* 229  
 \* *genjam* 127, 128, 140  
 \* *glabra* 127, 128, 147  
*gracilis* 240, 241, 248  
*grandis* 211, 220  
*haani* 136  
*hanoverana* 240, 251  
*insulana* 240, 241, 246  
*karnyi* 211, 226  
 \* *kevani* 110, 115

*kuekenthali* 127, 128, 145  
*lanceolata* 211, 220  
*leefmansi* 211, 240, 251  
 \* *longipennis* 127, 128, 142  
*luctuosa* 127, 128, 146  
 \* *manokwari* 127, 128, 142  
*marginata* 135, 145  
*marmorata* 240, 241, 254  
*multicolor* 110, 119  
*nigroreticulata* 127, 128, 135  
*novaeguineae* 211, 240, 242  
*nubila* 219, 222  
*var. obscura* (C. *rufo-*  
     [*femorata*]) 127, 132, 134  
 \* *ssp. occidentalis* (S.  
     [*marmorata*]) 241, 255  
*Opiptacris* 127, 149  
*Oxya* 135  
*patagiata* 123, 127, 128, 130  
*pervittata* 130  
*pictipennis* 127, 149  
*princeps* 240, 242  
*Pseudocranae* 137  
*punctipes* 229, 240, 256  
 \* *rammei* 110, 118  
 \* *rubra* 127, 128, 144  
*rufipalpis* 211, 240, 241, 245  
*rufipes* 127, 128, 141  
*rufofemorata* 127, 132  
 \* *samarensis* 110, 118  
*Segestes* 227 sqq  
*Segestidea* 240 sqq  
*Sexava* 218 sqq  
 \* *ssp. simulatrix* (S. *gracilis*)  
     [241, 250  
*soror* 240, 256  
*stibicki* 231, 235  
*Taeniophora* 136  
*tibialis* 127, 128, 132  
*trivittata* 127, 128, 140  
*tuberculata* 110, 112, 116  
*unicolor* 230  
*uniformis* 211, 240, 256  
*unistrigata* (tum) 127, 128,  
     [135, 151  
*vittaticeps* 227  
*willemsi* 110, 116  
 PLANTAE  
*Betula alba* 154

*Betula albo-sinensis* 181  
*Betula alleghaniensis* 180,  
     [181  
*Betula alnoides* 181  
*Betula apoensis* 181  
*Betula* × *borgraveana* 181  
*Betula celtiberica* 181  
*Betula chichibuensis* 181  
*Betula* × *coerulea* 181  
*Betula coerulea-grandis* 181  
*Betula corylifolia* 181  
*Betula costata* 180, 181  
*Betula cylindrostachya* 181  
*Betula davurica* 179, 181  
*Betula ermanii* 175, 180, 181  
*Betula forrestii* 181  
*Betula fruticosa* 181  
*Betula glandulifera* 181  
*Betula glandulosa* 181  
*Betula grossa* 180, 181  
*Betula* × *intermedia* 180,  
     [181  
*Betula humilis* 181  
*Betula jacquemontii* 180, 181  
*Betula kirghisorum* 181  
*Betula lenta* 180, 181  
*Betula litwinowii* 181  
*Betula maximowicziana* 181  
*Betula medwediewii* 181  
*Betula middendorffii* 181  
*Betula nana* 180, 181  
*Betula nigra* 181  
*Betula occidentalis* 153, 170,  
     [175, 180, 181  
*Betula papyrifera* 153, 170,  
     [177, 180, 181  
*Betula pendula* 153, 168, 174,  
     [177, 181  
*Betula platyphylla* 181  
*Betula populifolia* 170, 177,  
     [181  
*Betula pubescens* 174, 175,  
     [180, 181  
*Betula pumila* 181  
*Betula* × *purpusii* 161  
*Betula raddeana* 180, 181  
*Betula schmidtii* 181  
*Betula tatewakeana* 181  
*Betula turkestanica* 181  
*Betula utilis* 181  
*Cocos nucifera* 245, 251  
*Marasmius* 63

















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